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PREDATION OF JUVENILES OF THE HARD CLAM *MERCENARIA MERCENARIA* (LINNÉ) BY THE SNAPPING SHRIMP *ALPHEUS HETEROCHAELIS* SAY AND *ALPHEUS NORMANNI* KINGSLEY

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ABSTRACT   Two species of snapping shrimp, *Alpheus heterochaelis* and *A. normanni,* collected near Beaufort, North Carolina, during June 1982, and then held in the laboratory, used their major chelae to crush and consume juveniles of the hard clam *Mercenaria mercenaria.* Snapping shrimp (19.1 to 39.4 mm in total body length [TL]) ate clams in the largest size-class (15.1 to 20.0 mm in shell length), but preferred smaller clams when offered equal numbers in this large size-class and in each of three smaller size-classes. Female snapping shrimp, regardless of species, exhibited a statistically higher predation rate than males when the results of five separate experiments were combined. The major chelae of the females of specimens of *A. heterochaelis* ($>$32.0 mm TL) were smaller than those of equal size males. *Alpheus heterochaelis* (19.1 to 27.2 mm TL) had a larger major chela for a given body length than did specimens of *A. normanni;* however, predation rates of the two species were not significantly different. The number of clams crushed was related to both the size of the major chelae and total body length for *A. normanni,* but not for *A. heterochaelis. Alpheus* spp. inflict two types of shell damage which are identical to those caused by blue crabs. These results imply that previous studies may have overestimated the importance of crab predation and underestimated or ignored the importance of predation by snapping shrimp.

KEY WORDS: *Alpheus,* snapping shrimp, predation, *Mercenaria,* hard clams

INTRODUCTION

The hard clam or northern quahog *Mercenaria mercenaria* (Linné) is distributed along the Atlantic coast from the Gulf of St. Lawrence to the northern Gulf of Mexico and occurs intertidally down to 15 m (Menzel 1970). This species is harvested commercially throughout most of its range; e.g., during 1981 and 1982 in North Carolina, the hard clam fishery ranked third in importance of all commercial fisheries based on a dockside dollar value of $5.4 million and $6.6 million, respectively (Street 1982).

A progression of predators follows the growth of the hard clam from the earliest planktonic (Loosanoff 1959, Carriker 1961), post-settlement (Hunt 1981), and juvenile stages (Carriker 1951, Goodwin 1968, Whetstone and Eversole 1978) through adulthood (Carriker 1951, MacKenzie 1977, Greene 1978, Peterson 1982). As *M. mercenaria* increases in size so does its predators; because large predators are more commonly recognized in the field and have been studied extensively in the laboratory, their importance in regulating hard clam population sizes may have been over-emphasized. Investigations of predation on natural or hatchery-reared juvenile hard clams by blue crabs (*Callinectes sapidus* Rathbun) (Carriker 1951, Menzel and Sims 1964, Castagna and Kraeuter 1977), mud crabs (various xanthid genera) (Landers 1954, MacKenzie 1977, Whetstone and Eversole 1978), and miscellaneous species (Menzel et al. 1976) imply that those predators are responsible for the

majority of natural post-settlement mortality of hard clams. Resource managers and fishermen who operate commercial bottom leases should be aware of the potential effectiveness of these predators in reducing hard clam populations.

I conducted a series field experiments near Beaufort, NC, from August 1981 through April 1982, in which juveniles of *M. mercenaria* (6.0 to 15.0 mm in length) were maintained in cages designed to exclude large ($\geq$ 6.4 mm) epibenthic predators (Beal, unpublished data). Because numerous snapping shrimp were observed inside the field cages, which also contained several crushed juvenile hard clams, they were suspected of being an important additional consumer of juvenile clams.

As a result of these field investigations, I performed several laboratory experiments that clearly showed that two species of snapping shrimp, *Alpheus heterochaelis* Say and *Alpheus normanni* Kingsley, should be added to the list of known hard clam predators. Here I demonstrate that both species will crush and consume juvenile hard clams under laboratory conditions and provide field observations that indicate they do so in nature as well. Several factors are also examined:

1. Is size of snapping shrimp correlated with its predation rate?
2. Do shrimp show a size preference within the size-classes of clams they are able to crush?
3. Does sex or species of snapping shrimp affect predation rate?
4. Can clam mortality, caused by blue crabs, be distinguished from that inflicted by snapping shrimp on the basis of shell damage?

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MATERIALS AND METHODS

Snapping shrimp and shell debris were obtained from two oyster rocks (reefs) near Beaufort, NC, on 18 and 26 June 1982, using a suction dredge. Shell debris (hash) was the substrate used in all experiments and consisted of dead and fragmented oysters and clams greater than 3.0 mm (the smallest size the dredge efficiently captured). Juvenile hard clams were purchased from a commercial dealer and given a color dot (Mark-Tex Corp., paint) on both valves (near the umbo) which distinguished them from any dead clams within the shell debris.

Snapping shrimp and shell debris were brought to the laboratory on the same day they were collected. Shrimp were placed in glass finger bowls where they were given crushed hard clams as food. Bowls were placed in large tanks (75 × 75 × 30 cm) supplied with unfiltered seawater. No snapping shrimp were held longer than four days in the pre-experimental setting.

Shell debris was sieved through a 3.2-mm mesh to remove all fine sediments and small benthos at the beginning of each experiment. Any large animals were also removed before the shell debris was placed in finger bowls (20.0 cm dia; 6.5-cm depth) to a depth of 4 cm.

Forty marked clams were placed at a depth of 1 cm before one snapping shrimp was added to each bowl in each experiment. Nylon window screening (1.2-mm mesh) was placed over the top of each bowl and secured by an elastic band to ensure that the shrimp remained inside the bowl during the course of the experiment. Controls were employed to separate all types of shrimp-caused mortality from all other sources of mortality. The controls were treated identically to the other clams placed in finger bowls except they received no snapping shrimp.

Each tank held nine finger bowls and in experiments where more than one tank was used, treatment and control bowls were randomly assigned to tanks. The nylon tops were cleaned daily using hands to brush away accumulated silt; the bowls were not removed from the tanks. Snapping shrimp were removed from each bowl and the contents of the bowls were sieved through 1-mm mesh after one week. Recovered clams were separated into three categories: living, dead (empty, undamaged shells), or dead (crushed).

Table 1 shows the experimental interval, the number of replicate *Alpheus* spp. used, and the number of controls for each experiment. Experiments A through C were designed to test whether *A. heterochaelis* could crush and consume juvenile hard clams. The same two snapping shrimp were used in both experiments A and B. Replication was increased in experiments D and E because of the large variability in crushing rates of the snapping shrimp.

The major chela (MC) of each snapping shrimp was measured from the distal end of the dactylus longitudinally to the proximal end of the propodus, and total body length (TL) was measured from the rostrum to the telson after every experiment. These two morphological traits were measured to test whether the relationship between size of the MC and TL differed between sexes of large specimens of *A. heterochaelis* and between species of smaller snapping shrimp. In addition, I tested whether predation rate was related to either morphological trait.

TABLE 1.

The experimental interval, number of *Alpheus*, and number of controls for each experiment.

Experiment	Dates	Number of *Alpheus* spp. treatments	Number of Controls
A	18 June to 25 June	2 (*A. heterochaelis*)	2
B	25 June to 2 July	2 (*A. heterochaelis*)	2
C	26 June to 3 July	4 (*A. heterochaelis*)	2
D	29 June to 6 July	14 (*A. heterochaelis*)	3
E	30 June to 7 July	12 (*A. heterochaelis*)	3
		8 (*A. normanni*)	

Four size-classes of juveniles of *M. mercenaria* (6.0 to 8.0, 8.1 to 10.0, 10.1 to 15.0, and 15.1 to 20.0 mm in shell length [SL, the greatest anterior to posterior measurement]) were used to test if shrimp preferred clams within a certain size. Ten clams from each size category were placed in each bowl. A total of 20 large specimens of *A. heterochaelis* (mean TL = 34.1 mm ± 2.5 SD) was used in these experiments. To determine the effects of sex of snapping shrimp on predation rate, the nonparametric Wilcoxon two-sample test on total number crushed by individual snapping shrimp was used. Data from experiments A through D were combined because (1) the time interval for each experiment was identical (7 days); (2) there was no apparent effect of time on predation rate; and (3) size categories of juvenile hard clams, as well as number of clams used within each size category, were held constant. Mean total numbers crushed by individual shrimp were used from experiments A and B because the same shrimp were used in both trials. Total counts were used for individual shrimp in experiments C and D. Morphometric data from experiments A through D were combined and the lines expressing TL to MC for the 11 male snapping shrimp (Y = 2.99 + 0.487X; r^2 = 0.74) and 9 female snapping shrimp (Y = 5.03 + 0.323X; r^2 = 0.69) were compared using multiple regression analysis.

In experiment E, individuals of both species were smaller than those specimens of *A. heterochaelis* used in the previous experiments. Twelve specimens of *A. heterochaelis* (mean TL = 23.4 mm ± 2.6 SD) and eight specimens of *A. normanni* (mean TL = 24.0 mm ± 1.9 SD) were used. Clams from only two size-classes (4.5–8.0 mm and 8.1–10.0 mm) were used because of the small size of these snapping shrimp. Twenty clams from each size category were placed in each bowl. A Model I 2-way analysis of variance (ANOVA) was performed on numbers crushed to test the effects of species and sex of snapping shrimp on

predation rate. Numbers crushed (Y) were first transformed with $\ln(Y + 1)$ and a Bartlett's test (Sokal and Rohlf 1969) was performed to determine whether the transformation helped eliminate variance heterogeneity. Morphometric data from male snapping shrimp were pooled with data from female shrimp for each species in experiment E to determine whether the two species differed in their relation between TL and MC for the 12 specimens of *A. heterochaelis* ($Y = 2.71 + 0.382X$; $r^2 = 0.37$) and the 8 specimens of *A. normanni* ($Y = 3.55 + 0.493X$; $r^2 = 0.56$). Again, multiple regression analysis was used to compare lines.

Five specimens of *A. heterochaelis* were placed in isopropyl alcohol within 12 hours after feeding to test whether shell fragments pass through the cardiac stomachs of snapping shrimp. After one hour the cardiac stomach of each shrimp was excised and examined.

Temperature and salinity were monitored daily within each tank. Tanks never differed by more than $0.7°C$ or 1 ppt S on any given day. The temperature range for the entire experimental interval (18 June to 7 July) was 24.3 to $27.5°C$. The salinity range for the same time interval was 32 to 34 ppt S.

Four blue crabs, *Callinectes sapidus* Rathbun (carapace widths: 146.9, 136.7, 74.8 and 59.7 mm), were placed in separate seawater tanks ($25 \times 25 \times 30$ cm) without sediment but containing 40 juvenile hard clams (10 from each size category used in experiments A through D) to compare shell damage inflicted by *Alpheus* spp. with that described for crabs (Vermeij 1978). The crabs were used to test whether it is possible to correctly assign clam mortality to the proper predator on the basis of shell damage. Crabs remained in the tanks until at least 50% of the clams had been crushed. This took 3 days for the smallest blue crab and 3 hours for the largest.

RESULTS

Experiments A through D (Table 2)

No clam mortalities occurred in the control bowls, but a total of 77 clam deaths occurred in those bowls containing the snapping shrimp *A. heterochaelis;* in each case a chipped or crushed clam shell was recovered. This clearly demonstrates that snapping shrimp crush juvenile hard clams; furthermore, body tissues were removed from each valve indicating that the clams were eaten.

I observed a female of *A. heterochaelis* (35.2-mm TL) crush and consume a juvenile hard clam ($\simeq$ 8.0-mm SL) in a small finger bowl (10-cm, dia; 5-cm depth) containing no shell, other substrate, or other clams. The snapping shrimp grasped the clam near the umbo with the minor chelae, then lifted the clam several millimeters off the bottom. With the dactylus cocked, the snapping shrimp raised its major chela so that the clam was wedged (anterior to posterior and 2 to 3 mm ventral of the umbo) between the propodus and dactylus with its umbo and dorsal margin straight up. The dactylus closed quickly fracturing most of the clam,

leaving only a small portion of the umbo intact. Initially, the mantle held the fractured pieces of clam together, but after the shrimp used its minor chela to tear the mantle from the valve remnants, the small fragments of shell became separated. The shrimp then tore off pieces of body tissue and used its minor chela and pereiopods in feeding. The cardiac stomach of each snapping shrimp examined contained shell fragments and, in one case, the painted portion of the clam.

Female snapping shrimp accounted for 92% of all clams crushed in experiments A through D; however, this was not statistically significant ($P = 0.09$). Snapping shrimp showed a statistical preference for smaller juvenile clams in a chi-square (X^2) test ($X^2 = 34.8$, df = 3, $P < 0.001$); 49% of all the clams crushed and consumed belonged to the smallest (6.0 to 8.0-mm SL) size-class. Clams were eaten in all size-classes including the largest (15.1 to 20.0-mm SL).

The variances around the straight lines relating TL to MC for the 11 males and 9 females of *A. heterochaelis* (Figure 1) were not significantly different. The lines were parallel ($P > 0.75$), but not coincident ($P < 0.001$ in partial F-test). Analysis of covariance (ANCOVA) demonstrated that, even though females had a greater mean TL (35.41 mm) than males (32.95 mm), males had a larger MC for a given TL than females ($P < 0.001$). Because of the apparent effect of sex on predation rate in experiments A through D, sexes were not combined when I tested whether predation rate could be explained by either morphological trait. No significant relationships existed between TL ($r_\delta = 0.48$, n = 11; $r_\varphi = 0.14$, n = 9) or size of MC ($r_\delta = 0.52$, n = 11; $r_\varphi = 0.43$, n = 9) and predation rate.

Experiment E (Table 3)

One 5.6-mm SL clam died in a control bowl as a result of natural causes; however, 31 clams died as a result of crushing in bowls containing *A. heterochaelis* and 38 clams were crushed in bowls containing *A. normanni*. All 31 clams eaten by specimens of *A. heterochaelis* in experiment E belonged to the smaller size-class (4.5–8.0 mm); none were eaten in the larger size-class (8.1–10.0 mm) as were crushed and consumed by larger specimens of *A. heterochaelis* in experiments A through D. Similarly, 95% of those clams crushed and consumed by *A. normanni* came from the smaller size category. Bartlett's test demonstrated that the logarithmic transformation reduced variance heterogeneity and the Model I 2-way ANOVA resulted in no species $\times$ sex interaction ($P > 0.50$) or effect of species ($P > 0.75$). The 15 female snapping shrimp ate 67 of the 69 (97%) clams; the remaining 2 crushed clams were eaten by one of the five male shrimp. This was not statistically significant ($P = 0.065$).

The straight lines relating TL to MC (Figure 1) from experiment E had equal variances ($P > 0.05$) and were parallel ($P > 0.75$), but not coincident ($P < 0.001$ in a partial F-test). Application of ANCOVA yielded a significant difference ($P < 0.001$) in the adjusted MC lengths between

TABLE 2.

Results of Experiments A through D in which *Alpheus heterochaelis* was exposed for
7 days to 10 clams in each of four size categories.

Experiment	Sex	TL* (mm)	MC† (mm)	Number Crushed Within a Size Category (mm)				Total Crushed	Number Alive
				6.0–8.0	8.1–10.0	10.1–15.0	15.1–20.0		
A	M	34.8	20.1	0	0	0	0	0	40
	F	38.4	17.6	6	7	2	1	16	24
	Control 1			0	0	0	0	0	40
	Control 2			0	0	0	0	0	40
B	M	34.8	20.1	1	0	0	0	1	39
	F	38.4	17.6	5	2	3	0	t0	30
	Control 1			0	0	0	0	0	40
	Control 2			0	0	0	0	0	40
C	M	32.4	18.7	0	0	0	0	0	40
	M	34.0	19.9	0	0	0	0	0	40
	F	34.0	15.9	0	0	0	0	0	40
	F	35.2	16.4	9	7	8	1	25	15
	Control 1			0	0	0	0	0	40
	Control 2			0	0	0	0	0	40
D	M	29.9	17.2	0	0	0	0	0	40
	M	30.0	17.2	0	0	0	0	0	40
	M	30.4	18.0	0	0	0	0	0	40
	M	30.9	19.0	0	0	0	0	0	40
	M	34.4	19.9	1	0	0	0	1	39
	M	34.6	19.9	0	1	0	0	1	39
	M	34.9	18.5	2	0	t	0	3	37
	M	35.9	21.1	0	0	0	0	0	40
	F	32.1	16.2	4	1	0	0	5	35
	F	33.5	15.6	0	0	0	0	0	40
	F	35.0	16.3	0	t	0	0	t	39
	F	35.3	15.4	1	0	0	0	t	39
	F	35.8	16.6	0	0	0	0	0	40
	F	39.4	t8.1	9	3	1	0	13	27
	Control 1			0	0	0	0	0	40
	Control 2			0	0	0	0	0	40
	Control 3			0	0	0	0	0	40
Total number of controls				0	0	0	0	0	360
Total number of males				4	1	1	0	6	474
Total number of females				34	21	14	2	7t	329

*TL = total body length
†MC = length of major chela

species. *Alpheus heterochaelis* in the size range 19.1 to 27.2 mm had a larger MC for a given TL than *A. normanni*. There was no significant (P > 0.05) relationship between either TL (r = −0.24, n = 12) or length of MC (r = −0.05, n = 12) and number of clams crushed by *A. heterochaelis*; however, predation rate was significantly (P < 0.05) correlated for TL (r = 0.76, n = 8) and MC size (r = 0.77, n = 8) for *A. normanni*.

Effect of Sex on Predation Rate

Fischer's technique of combining probabilities from independent tests of significance (Sokal and Rohlf 1969) was applied to test the effect of sex of snapping shrimp on predation rate from all experiments. This test resulted in a significant (P = 0.04) overall effect of sex implying that females had a greater crushing rate over all experiments. The effect of sex in experiment E included information from both species; however, because there was no species × sex interaction, this test was justified over all experiments. The size distributions of males and females used in all experiments were compared because size of snapping shrimp may influence predation rate. Size of snapping shrimp was statistically independent of sex ($X^2 = 9.38$; df = 6; P = 0.195) over all experiments.

Shell Damage Inflicted by Snapping Shrimp (Figure 2) and Blue Crabs

Two types of shell damage caused by snapping shrimp were distinguished by visual inspection. In the first (Type I)
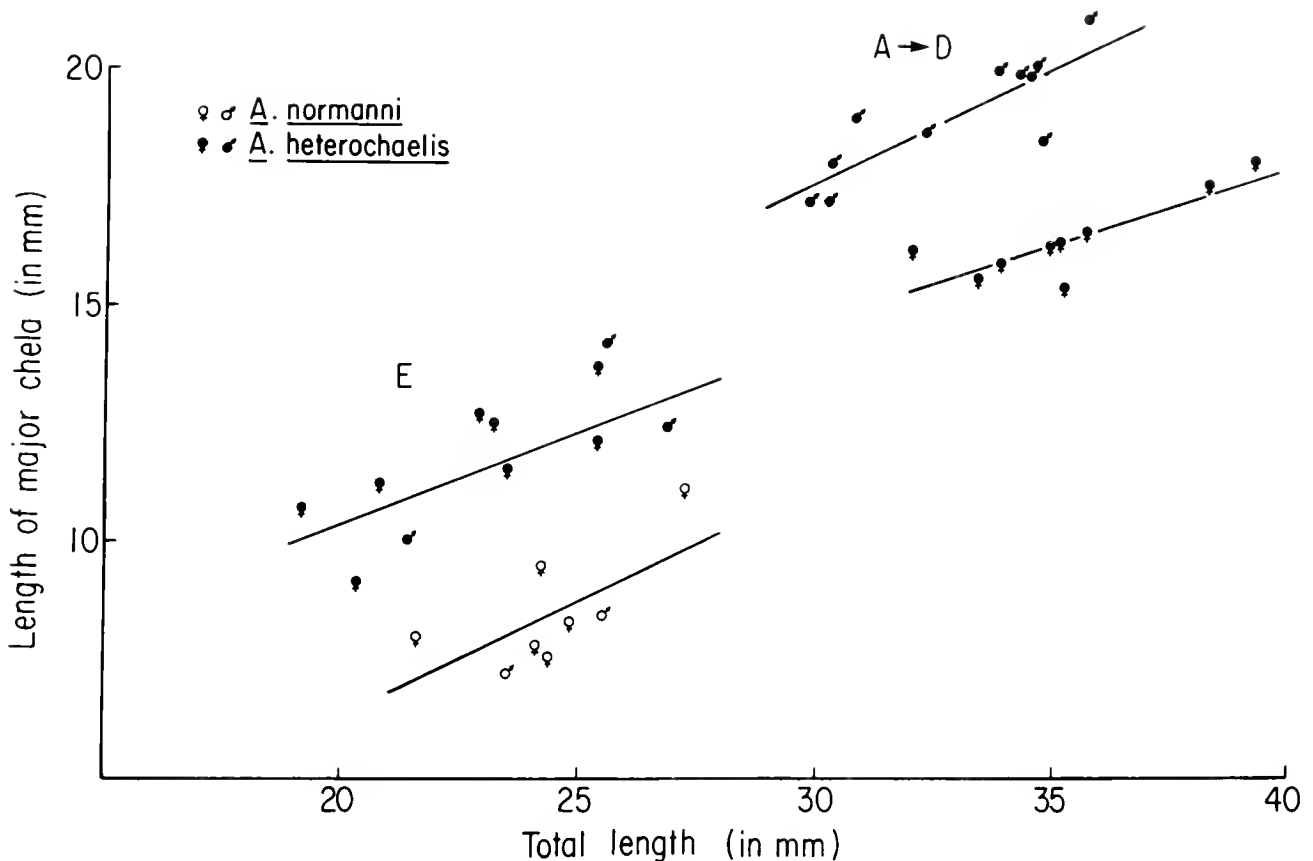
Figure 1. Relationships between total body length (TL) and size of major chela (MC) for snapping shrimp used in all experiments. Capital letters refer to experiment. Open circles: *Alpheus normanni;* closed circles: *Alpheus heterochaelis.*

at least one of the valves remained intact. Shell chips or fractures were restricted along the posterior edge and often both valves had symmetrical chips. Where both valves were not chipped identically, one valve was chipped along the posterior edge while damage to the other valve ranged from restricted ventral margin fractures to an extensively broken valve having only the umbo region intact. Valves exhibiting damage of the second type (Type II) had been completely crushed and only the immediate area around the umbo was left intact and held together by the hinge ligament (Figure 2).

To learn if shell damage inflicted by snapping shrimp and blue crabs was distinguishable, crushed shells from experiments A through D and from the blue crab experiment were collected and separated by size-class into damage types. Both predators caused Type I and Type II damage in each size-class. Sixty clams were crushed by *A. heterochaelis* in the size range 6.0 to 10.0 mm; 92% exhibited Type II damage, whereas 53% of the crushed clams between 10.1 and 20.0 mm exhibited Type I damage. Type II damage occurred in 70% of the juvenile hard clams (6.0 to 10.0 mm SL) crushed by blue crabs, whereas 8% of the crushed clams between 10.1 and 20.0 mm suffered Type I damage from blue crabs.

DISCUSSION

Experiments A through E demonstrate that two species of snapping shrimp, *A. heterochaelis* and *A. normanni,* can crush and consume juveniles of *M. mercenaria* and can also discriminate between sizes of prey when offered a choice. It is sometimes difficult to relate laboratory experiments to field experiments because the number of variables permitted to vary in each is different (Dayton and Oliver 1981); however, two observations from my caging study in the field suggested that snapping shrimp do indeed prey on juvenile hard clams (6.0 to 15.0 mm SL) in nature. Snapping shrimp were found inside complete 1 m² cages (6.4-mm mesh; see Beal [1983] for a detailed cage description) designed to keep large, epibenthic predators from preying on juvenile hard clams (Beal, unpublished data). When the contents of these cages were sieved in November 1981 and in April 1982, I found live clams as well as shell fragments which were identical in appearance to those clams crushed and consumed by *Alpheus* spp. in this study. No other predators or signs of predators were observed inside complete cages.

Female snapping shrimp exhibited a higher predation rate than did males over all experiments; however, the mechanism for this behavior was not investigated. Elner and

TABLE 3.

Results of Experiment E in which *Alpheus heterochaelis* and *Alpheus normanni*
were exposed for 7 days to 20 clams in each of two size categories.

Species	Sex	TL* (mm)	MC† (mm)	Number Crushed Within a Size Category (mm)		Total Crushed	Number Alive
				4.5–8.0	8.1–10.0		
Alpheus heterochaelis	M	21.4	10.0	0	0	0	40
	M	25.4	13.7	0	0	0	40
	M	26.9	12.4	2	0	2	38
Total males				2	0	2	118
	F	19.1	10.7	5	0	5	35
	F	20.3	9.1	0	0	0	40
	F	20.8	11.2	10	0	10	30
	F	22.9	12.7	0	0	0	40
	F	23.2	12.5	3	0	3	37
	F	23.5	11.5	3	0	3	37
	F	24.2	9.5	2	0	2	38
	F	25.6	14.2	2	0	2	38
	F	26.9	12.1	4	0	4	36
Total females				29	0	29	331
Total *A. heterochaelis*				31	0	31	449
Alpheus normanni	M	22.5	7.2	0	0	0	40
	M	23.4	7.6	0	0	0	40
Total males				0	0	0	80
	F	21.6	8.1	7	0	7	33
	F	23.1	7.8	0	0	0	40
	F	23.4	7.6	0	0	0	40
	F	23.8	8.3	0	0	0	40
	F	26.1	8.1	13	1	14	26
	F	27.2	11.1	16	1	17	23
Total females				36	2	38	202
Total *A. normanni*				36	2	38	282
Control 1				1	0	0	39
Control 2				0	0	0	40
Control 3				0	0	0	40

*TL = total body length
†MC = length of major chela

Hughes (1978) examined the diet of the shore crab *Carcinus maenus* (Linnaeus) and, to avoid potential biases caused by sexual differences in morphology and predatory behavior, used only male crabs. Here both sexes were used and, at least for larger specimens of *Alpheus heterochaelis*, females had a smaller major chela than did males of a similar body length. Because the major chela is used in crushing juvenile hard clams, males should have had the highest predatory rate. Ennis (1973) found a difference in the feeding activity between sexes of the American lobster *Homarus americanus* Milne Edwards; females continued to feed at a higher level longer into the winter than did males. Ennis (1973) suggested that this may have been caused by greater physiological demands on the female due to gonadal development. If an energetic explanation were true for snapping shrimp, similar experiments using females with developing versus developed gonads or, perhaps, immature (juvenile) versus mature females as well as males would be needed.

Accounts of snapping shrimp as predators are rare. Hazlett (1962) determined that a species of *Alpheus* from Bermuda was omnivorous. Goldberg (1971) studied a species of *Synalpheus* in the Florida Keys which preyed upon the gastropod *Coralliophila caribaea* Abbott without crushing it. The shrimp lifted the flexible operculum with its major chela exposing the gastropod while the minor chela tore off pieces of the foot. I am unaware of any account of predation by either *A. heterochaelis* or *A. normanni* on a bivalve mollusc.

Previous investigations concerning the role that the major chela plays in the behavior and ecology of these snapping shrimp suggest that it is used agonistically during intra- and interspecific interactions (Nolan and Salmon 1970, Schein 1977). Conover and Miller (1978) described the importance of the major chela in determining the success of a shrimp in competing for shelter. Glynn (1976) described a species of snapping shrimp off the Pacific coast of Panama

Figure 2. The size range of the five size-classes of juvenile hard clams and the shell damage caused by *Alpheus heterochaelis* from experiment A through F. Damage in the smaller size-classes was similar for both species. Each tick mark represents 1 mm.

which repulsed the crown-of-thorns sea star and prevented it from preying on a branching coral. In this study the major chela of *A. heterochaelis* (29.9 to 39.4 mm TL) was smaller in females compared with equal size males. Nolan and Salmon (1970) noted this sexual dimorphism in both species. They showed that when a female approached a larger male, she was threatened and quickly retreated because of aggressive male snapping; if the TL of a female was greater than that of the male she approached, the encounter would continue until cues important in sexual discrimination could be exchanged.

Whetstone and Eversole (1978) investigated the predators of juvenile hard clams in a South Carolina sound. They collected 13 species of crustaceans from subtidal and intertidal trays containing juvenile hard clams over a 19-month interval and examined their gut contents. They concluded, on the basis of shell fragments in the cardiac stomachs (as well as overall numbers collected), that the xanthid crab *Panopeus herbstii* Milne Edwards (1,465 collected from May 1975 through December 1976) was the most important predator of juvenile hard clams. *Alpheus heterochaelis* was the second most abundant crustacean found by Whetstone and Eversole (184 collected during that same time interval); nine specimens of *A. normanni* were also collected during that study. Whetstone and Eversole (1978) found no shell fragments in either species of *Alpheus* they examined and, on this basis, concluded that snapping shrimp were not hard clam predators; however, shell fragments were found in the cardiac stomachs of every snapping shrimp I examined. There may be several reasons why shell fragments were found in the cardiac stomachs of the snapping shrimp from this study and not in Whetstone and Eversole's (1978) investigation:

1. The snapping shrimp they collected may not have crushed any juvenile hard clams; Whetstone and Eversole (1978) used hard clams with a mean SL of 13 mm (however, 19% of the hard clams consumed in my experiments A through D were 10.1 to 15.0 mm SL [Table 2]);
2. The snapping shrimp may have been collected or preserved after evacuation of the cardiac stomachs had occurred; or
3. The shell fragments may have dissolved in the 10% formalin solution they used as a preservative.

The results presented in this paper suggest that *Alpheus* spp. may be an important predator of juveniles ($\leq$ 20.0 mm SL) of *M. mercenaria* in South Carolina sounds.

I have seen or heard snapping shrimp in a variety of areas in Bogue, Back, and Core sounds in North Carolina. These areas have several aspects in common. They either have muddy substrates with natural shelters such as living or dead oysters, or seagrass beds. Nolan and Salmon (1970) collected both species near Beaufort among clumps of oyster shells, as well as in eelgrass beds. *Alpheus heterochaelis* was more often found in muddy areas associated with clumps of oysters; *A. normanni* was found primarily in eelgrass beds. Hoff Stuart (National Marine Fisheries Service, Beaufort, NC, pers. comm.) found a mean of 6.1 adults of *A. normanni* and 1.1 adults of *A. heterochaelis* (TL $>$ 20.0 mm) per m^2 in a Back Sound eelgrass bed during 1975–1976. The mean number of clams consumed per snapping shrimp per day in my laboratory experiments was 0.72. This figure is indicative of clams $\leq$ 15.0 mm SL because only two clams were consumed that were $\geq$ 15.0 mm SL. Thus, if that rate is representative of their hard clam predation in nature, snapping shrimp of this size in that eelgrass bed may consume approximately 125 clams (4.5 to 15.0 mm SL) per m^2 per month.

The type of shell damage inflicted by these snapping shrimp is typical of crabs (Vermeij 1978). Cake (1970) found that *C. sapidus* could open large specimens of the sunray venus clam *Macrocallista nimbosa* (Lightfoot) without breaking their shells by "inserting the finger and cutting the adductor muscles." That type of shell damage by *Callinectes*, which leaves behind minute scars of cheliped activity on the periostracum, was not observed in this study; in fact, both snapping shrimp and blue crabs inflict similar types of shell damage. The entire clam is either broken into bits leaving only the umbo region, or is marginally damaged with chips occurring around the posterior edge of at least one valve. According to the results of this study, past investigations in which clam mortalities were assigned a particular crushing predator based on shell damage may have overestimated the importance of crab predation and underestimated or ignored the importance of predation by snapping shrimp. Furthermore, commercial clam culturists need to be concerned about protecting seed clams from snapping shrimp as well as from crabs and other predators. The spatial distribution and abundance of the bottom-dwelling snapping shrimp, as well as their natural predation rates on small hard clams, must be determined to fully assess the importance of these findings.

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SEASONAL GONADAL DEVELOPMENT OF YOUNG LABORATORY–SPAWNED SOUTHERN (*MERCENARIA CAMPECHIENSIS*) AND NORTHERN (*MERCENARIA MERCENARIA*) QUAHOGS AND THEIR RECIPROCAL HYBRIDS IN NORTHWEST FLORIDA

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ABSTRACT   The seasonal gonadal development of laboratory-spawned southern and northern quahogs and their reciprocal hybrids was investigated. All young clams were males and one or more stages of gametogenic activity were seen each month of the year. Winter spawning, which occurred in all pedigrees of quahogs, was considered abnormal and resulted from the unusually warm winter of 1974–75. Gonadal development of the hybrid ♀*Mercenaria campechiensis* × ♂ *Mercenaria mercenaria* was similar to its southern parent; the reciprocal hybrid was similar to its northern parent. This may indicate maternal influence. Little or no spawning by *M. campechiensis* during warmer months was unlike that of the other three pedigrees. Temperature was the overall controlling factor in gonadal development and spawning, but genetic differences existed between the two species.

KEY WORDS·   Genetics, gametogenesis, hybridization, hard clams, quahogs, *Mercenaria* spp.

INTRODUCTION

The seasonal gonadal development of the northern quahog clam *Mercenaria mercenaria* (Linné) has been studied from the New England area (Loosanoff 1937a,b), from Delaware Bay (Keck et al. 1975), from North Carolina (Porter 1964), and from South Carolina (Eversole et al. 1980). A closely related species, the southern quahog *Mercenaria campechiensis* (Gmelin), hydridizes readily with the northern quahog (Loosanoff 1954) and the hybrids are fertile (Menzel and Menzel 1965, Menzel 1968), but the reproductive cycles of neither the southern nor the hybrids have been investigated. The present study is of the seasonal gonadal cycles of young, laboratory-spawned northern and southern quahogs and their reciprocal hybrids cultured in northwestern Florida. The results are compared with published reports from other areas.

MATERIALS AND METHODS

Southern quahogs, previously collected in the vicinity of Florida State University (FSU) Marine Laboratory, northwestern Florida, were spawned by Dr. Charles Epifanio at the University of Delaware Center for Mariculture Research on 2 April 1974. Wild northern quahogs from Delaware Bay were also spawned. Besides making self-fertilizations of each species, reciprocal hybrids between the species were produced. The larvae were cultured to metamorphosis and grown to a size of 1 to 2 mm before shipment to Florida in late June 1974. The clams were reared to a size of 4 to 8 mm at the FSU Marine Laboratory. On 4 October 1974, they were planted in 10-cm deep, sandfilled, screen-covered

wooden boxes in Alligator Harbor, about 8 km from the laboratory. At mean low water 4 to 5 cm of water covered the clams.

Ten clams of each pedigree were sampled on the 5th (± 1 day) of each month from 6 November 1974 through 5 November 1975, and additional samples were taken on the 20th (± 1 day) in December 1974, and in September and October 1975. The total sample included 660 clams from which 6,000+ follicles were microscopically examined. After February 1975, the stock of the hybrid ♀ *Mercenaria mercenaria* × ♂ *Mercenaria campechiensis* was depleted, primarily from crab predation. Additional clams of the same pedigree, planted as surplus in the same area, were sampled from May 1975 until the stock became exhausted by August 1975.

Shucked clams were preserved in Bouin's fixative, transferred to alcohol, imbedded in Paraplast®, sectioned at 8 μm, mounted on slides, and stained with Erlich's hemotoxylin and erosin following standard histological procedures. Previous examinations showed that transverse midlongitudinal sections gave a good representation of the gonad condition. All follicles in the most representative of 8 to 10 sections of each clam were used to determine gonadal condition.

Determination of gonadal condition followed that of Ropes (1968) as modified by Haines (1976). As noted by Loosanoff (1937a), different follicles within the same clam and different clams within the same population were often in several stages of gonadal development. The gonadal stages are not illustrated because they have been reported previously by Loosanoff (1937a), Porter (1964), Keck et al. (1975), and Eversole et al. (1980). Brief descriptions of each stage follow.

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Indifferent or Spent

The lumen of the indifferent or spent follicles are usually conspicuously empty, although a few residual spermatozoa may be present (in spent follicles) and a few scattered spermatogonia occur around the membranes of the otherwise bare follicles.

Early to Late Active

Follicles in the early active stage are undergoing primary and secondary spermatogenesis, with a nearly continuous layer of cells forming around the follicle membrane. Later, the lumen fills with basophilic spermatids and a few spermatogonia occur near the periphery. Early and late active stages were recorded separately but are presented as active stage only.

Ripe

The ripe phase is easily distinguished by a dense mass of spermatozoa, filling the follicles. Other types of gametogenic cells may be present, but are not abundant.

Partially Spent

Partially spent follicles contain spermatozoa within the lumen of the follicle but these are substantially less abundant than in the ripe stage.

Percentages of each gonadal stage for each pedigree at each sampling were graphed and the mean percentages of each stage of each pedigree were calculated and graphed to emphasize the similarities and differences between the four pedigrees. The first samples (November 1974) were not included in the mean calculations because no clams were mature enough to spawn and the results would be biased. Additionally, because of the smaller amount of data for the hybrid ♀ *Mercenaria mercenaria* X ♂ *Mercenaria campechiensis*, comparative data were recalculated using only samples collected in November 1974–February 1975, and May–August 1975.

Water temperatures were taken at time of sampling at depths of 20 to 30 cm. These infrequent observations were supplemented with minimum and maximum air temperatures (mean of 6-day intervals) from local climatological data recorded at Apalachicola, FL (NOAA 1974a, 1975a). Although Apalachicola is about 50 km from Alligator Harbor, that coastal location has the same latitude and is considered representative for this study.

In April 1976, when the clams were two years old, the remaining 19 southern, 4 northern and 11 hybrids (♀ *Mercenaria campechiensis* X ♂ *Mercenaria mercenaria*) were recovered and their sex was determined by the smear technique.

RESULTS

Both of the species and the hybrids were predominantly male. Two clams (0.3%) showed evidence of oogenesis. The follicles were in the early active stage, but no clams were observed with ripe female follicles. Occasionally, a few early stage female gamete cells occurred in otherwise male follicles, indicating a possibility for hermaphroditism. Gametogenesis had commenced by the first examination in November 1974, when the quahogs were seven months old, but only 2 to 4 follicles were seen per histological section. Later, the number of follicles increased to 15 to 20 per section. Gametogenesis in one or more stages were seen throughout the entire period in all the samples and pedigrees. Differences in the seasonal occurrence and relative overall abundance of each stage occurred in each pedigree. A discussion of the seasonal occurrence of each gonadal stage and probable times of spawnings are given for each pedigree.

Southern Quahog, Mercenaria campechiensis

Indifferent or spent follicles were present in all the samples of the southern quahog (Figure 1) and were in the largest mean percentage, 54% (Figure 2A). Active stages were also seen in all the samples except that taken 5 April, but occurred in low percentages in December, May, and June, with values of 10, 5, and 6%, respectively (Figure 1). The mean percentage for the entire period was 23% (Figure 2A). The percentages of ripe stage follicles were highest in both samples taken in December (47% and 40%) and in January (43%). This stage decreased in February (10%), March (14%), and April (6%), and none or very low percentages occurred through the 20 September sample (6%). Ripe follicles were found in the remaining samples (9–14%) (Figure 1). The mean for the entire period was 13% (Figure 2A). Partially spent stages were first seen in the sample taken 20 December (9%) and continued in relatively high percentages through the 5 April period (10–32%). This stage decreased by the May sample (6%) and was low until the following fall, increasing to 17% on 5 October (Figure 1). The mean was 10% (Figure 2A).

Spawning, as indicated by comparison of ripe and partially spent stages, commenced after the 5 December sample and continued until 5 April, with a probable peak in March. Little or no spawning occurred during the summer months, but spawning commenced again after 5 September.

Northern Quahog, Mercenaria mercenaria

Indifferent or spent follicles were present in all samples of *Mercenaria mercenaria* (Figure 1) but in considerably less abundance ($\bar{X}$ = 28%) than for the southern species (Figure 2A). Active stage follicles were also present in all samples ($\bar{X}$ = 58%) and in greater abundance than the southern species (Figure 2A). Ripe follicles occurred in all sampling periods, except the first on 6 November and those on 5 May and 20 September (Figure 1) ($\bar{X}$ = 10%) (Figure 2A). Partially spent follicles were seen in the samples taken 5 and 20 December, but not again until 5 March, when the highest percentage occurred (13%). This stage occurred on all the other sampling dates except that taken on 5 May (Figure 1). The mean was 4% (Figure 2A).
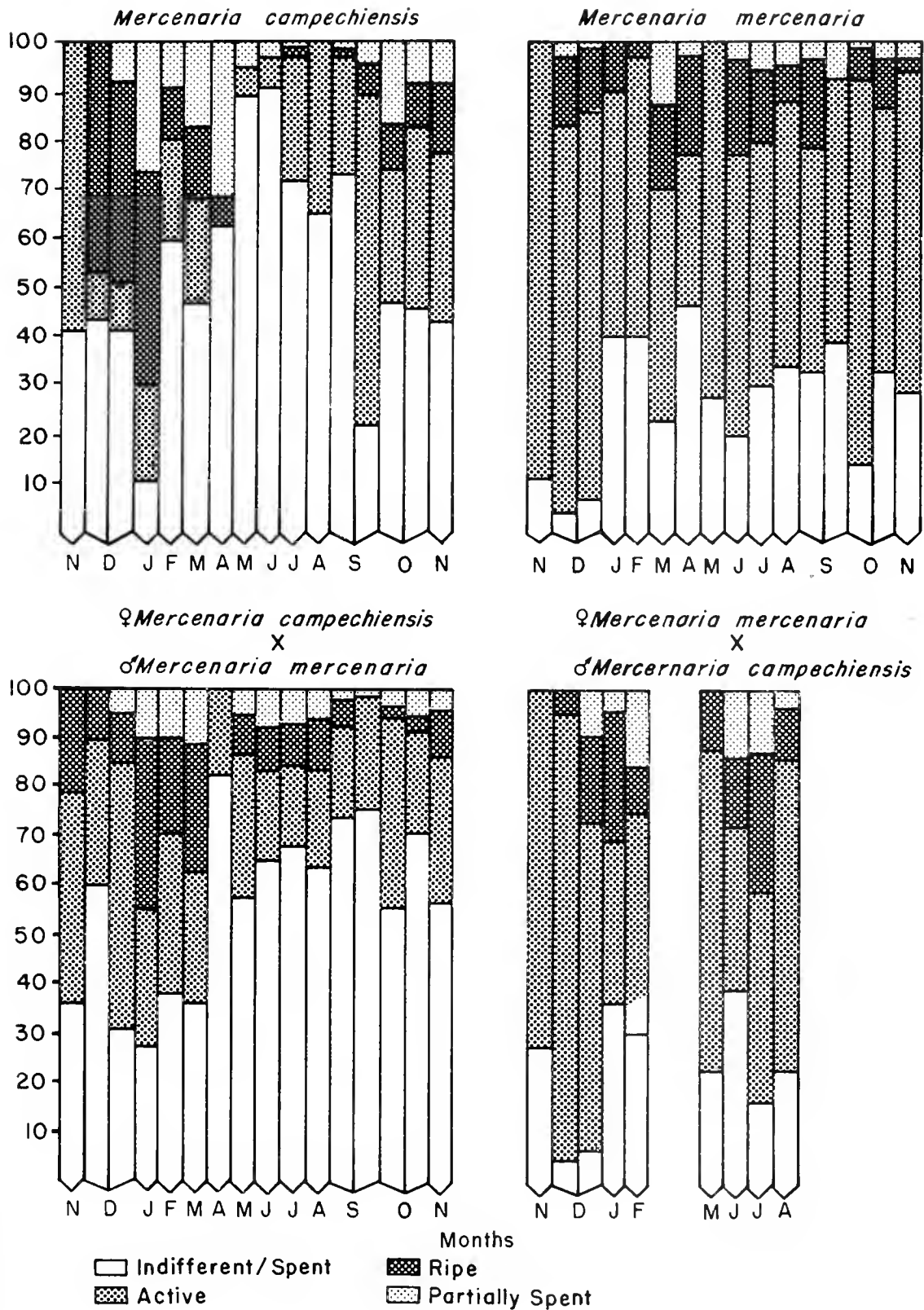
Figure 1. Reproductive cycles of southern and northern quahogs and their hybrids (660 total) shown as the percentage of follicles (males only) in each gonadal stage (period from 6 November 1974 through 5 November 1975).
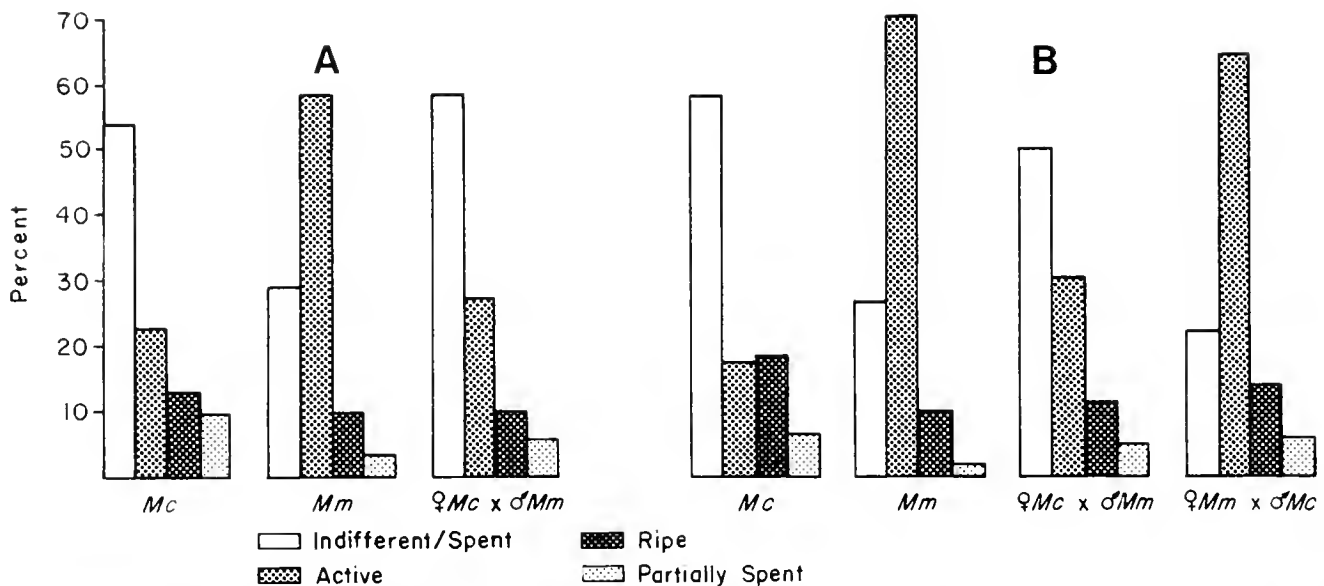
Figure 2. Mean percentages of follicle stages in southern (*Mc*) and northern (*Mn*) quahogs and their hybrids. (A) December 1974–November 1975: southern, northern and ♀ southern ✕ ♂ northern. (B) December 1974–February 1975 and May–August 1975: southern, northern and reciprocal hybrids.

The data for ripe and partially spent follicles indicate that spawning started by 5 December, but ceased from 20 December until after the 5 February sample. A peak of spawning occurred between 5 February and 5 May, with a probable high in March. Spawning resumed after 5 May and continued throughout the balance of the sampling period; a probable secondary peak occurred in September.

Hybrid, ♀ Mercenaria campechiensis ✕ ♂ Mercenaria mercenaria

The sequences of follicle development stages in the hybrid ♀ *Mercenaria campechienses* ✕ ♂ *Mercenaria mercenaria* are similar to the southern quahog parent. Indifferent or spent stages were found in all the samples (Figure 1) and, as in *M. campechienses*, had the highest mean (58%) (Figure 2A). Active follicle stages were also present in all the samples, ranging from a high of 54% on 20 December to lows of 17% in April, June, and July (Figure 1); the mean for the entire period was 27% (Figure 2A). This hybrid was the only pedigree that had ripe follicles (21%) on the first sampling (6 November 1974). The highest percentages of the ripe stage occurred on 5 January (34%) and on 5 March (26%). Ripe follicles were not seen in the 5 April samples but were observed in varying percentages for the balance of the sampling dates (Figure 1). The mean of the ripe follicles was 10% (Figure 2A). Partially spent stages were first seen 20 December and continued through the 5 March sample; none occurred on 5 April. This stage occurred in low percentages for the balance of the period, except for none on 20 December (Figure 1). The mean was 5% (Figure 2A).

The data indicate that spawning commenced after 5 December and continued through March. The absence of both ripe and partially spent stages in the 5 April sample

indicates a peak of spawning in March. Spawning resumed after 5 April and continued throughout the balance of the examinations, with probable peaks in May–July and again in September.

Hybrid, ♀ Mercenaria mercenaria ✕ ♂ Mercenaria campechiensis

Unfortunately data for the hybrid ♀ *Mercenaria mercenaria* ✕ ♂ *Mercenaria campechiensis* are incomplete, but those obtained show the sequences of follicle development to be similar to the northern quahog. Indifferent or spent stages were present in all the samples and ranged from a high of 40% on 5 June to a low of 5% on 5 December (Figure 1) ($\bar{X}$ = 23%, Figure 2B). Ripe follicles (4%) first seen on 5 December, increased to a high of 26% on 5 January, and were found on all the other dates for which data are available; another high (28%) occurred on 5 July (Figure 1). The mean for the entire period was 15% (Figure 2B). Partially spent follicles were first observed on 20 December and were seen in all the other samples, except that on 5 May (Figure 1); $\bar{X}$ = 7% (Figure 2B).

Spawning commenced after 5 December and continued to at least 5 February. The absence of partially spent follicles on 5 May indicates that a peak of spawning occurred prior to this date. Spawning continued after 5 May to at least 5 August, the last date sampled.

Sex could be determined for only 15 of the 34 two-year-old clams collected in April 1976. Of these clams, 13 were males and 2 were females (2 of 4 northern sampled).

DISCUSSION

This is the first study of the seasonal gonadal development of the southern quahog *Mercenaria campechiensis* and

its hybrids with the northern species *Mercenaria mercenaria,* with a comparison of laboratory-spawned clams of known age grown in the semitropical area of northern Florida. This study is not as thorough as those from more northern latitudes because observations were made for only one year and of male clams only. The spawnings that occurred in the winter period were undoubtedly atypical and are discussed in more detail below.

Loosanoff (1937a) found that quahogs have a protandric development; almost all clams (98%) developed first as males, but eventually achieved an equal sex ratio as older clams. Eversole et al. (1980) also found a preponderance of males to females (9.5:1) in young quahogs and a 1:1 sex ratio in older animals. Our study confirms the protandric development in northern quahogs and documents the same type of development in the southern species and its hybrids. The samples of 2-year-old clams revealed that sex reversal to female was occurring, even though the sampling was very small. Large clams of both species and hybrids that were used in our spawning experiments over the past 20 years usually had a 1:1 sex ratio.

Only 2 to 4 follicles were present in the first sample (6 November 1974) and were localized near the stomach ventral of the pericardial sinus. This was the same location reported by Loosanoff (1937a), but he found 6 to 8 follicles in clams of approximately the same size and probably of lesser age. The slighter gonadal development of quahogs grown in Florida was surprising, especially as growth rates have been reported to be greater than in more northern areas (Menzel 1961, 1962, 1977). One possible explanation is that the animals were laboratory reared and cultured in the natural habitat for only one month when first examined. Growth has always been less under our laboratory conditions than when planted in the open waters. Enough food may have been available for shell growth but not enough for gonadal development. Sastry (1966) stated that the bay scallop *Argopecten irradians* (Lamarck) "requires large amounts of food for gonad growth." Loosanoff and Davis (1950) found that *Crassostrea virginica* (Gmelin) did not mature sexually with poor glycogen reserve.

Figures 1 and 2, especially 2, show a usually low percentage of the partially spent stage in all the pedigrees. This probably indicates that once spawning is initiated in ripe clams, it is completed in a short period of time. If partially spent follicles occur for only a brief period, errors may have been made in deducing times of spawning, which were based on comparisons of ripe and partially spent clams at each examination (1 month in most instances).

Spawning throughout the year in marine invertebrates occurs most commonly in areas where there is little seasonal change, such as the tropics, polar regions, and deep sea (Goodbody 1965, Sanders and Hessler 1969). Northwestern Florida is subtropical, but warmer than normal temperatures occurred during the winter of 1975–75. Northern Florida experiences periods of air temperatures below

freezing and water temperatures below 10°C; water temperatures in January-February 1958–61 were as low as 6 to 9°C (Menzel 1961). The lowest water temperature during the winter of 1974–75 was 11.5°C in early December and air temperatures at Apalachicola never dropped below freezing (Figure 3). Extended periods occurred during the winter of 1974–75 when air temperatures were above 20°C in December-February (Figure 3). Those periods coincided with minus spring tides of −5 to −40 cm during the hours of 0730–1700 (National Oceanic and Atmospheric Administration, 1974b, 1975b). We have repeatedly observed in our laboratory that when alternating thermal stimulation is used to induce spawning, quahogs initiate spawning on the decreasing temperatures. Also, males usually spawn before females. The male quahogs in the boxes may, therefore, have been warmed to the critical spawning temperatures during the minus tides on warm days and stimulated to spawn when covered by the cooler incoming water at flood tide.

All quahog pedigrees had ripe follicles during winter months. This is consistent with other observations. Chestnut (1951) found that *Mercenaria mercenaria* often reach sexual maturity by mid-winter in North Carolina. Our thermal-induced laboratory spawning of both sexes has been most successful during the winter months. Winter spawnings are unusual in northern Florida. All wild quahogs have been found subtidally; a few may be uncovered by low tides of > −30 cm. Even if winter spawning does occur, it is unlikely that the gametes/larvae would survive in the relatively cold water. A larger percentage of the follicles may have been in the ripe condition during the winter months if normal temperatures had prevented spawning.

Reproductive cycles in marine invertebrates vary with the latitude and modifications have been associated with differences in temperature regimes (Orton 1920, Nelson 1928, Thorson 1950, Loosanoff and Nomejko 1951, Sastry and Blake 1971). The northern quahog ranges from Canada southward on the Atlantic coast and throughout the northern Gulf of Mexico (Abbot 1974) and thus experiences a wide range of temperatures. The spawning periods of the northern quahog have been documented for the areas ranging from Long Island Sound to South Carolina and now for northern Florida. The spawning periods in Florida, disregarding the winter spawning, showed bimodal spawning peaks in the spring and fall similar to that observed in the Carolinas (Porter 1964, Eversole et al. 1980); however, spawning began about a month (March) earlier and extended about a month (October) later than in the Carolinas. These northern clams were the progeny of clams native to Delaware Bay, where there is a single peak of spawning (Keck et al. 1975), similar to Long Island Sound (Loosanoff 1937b). Peak spawnings by southern and northern quahogs and the reciprocal hybrids were essentially the same.

We noted that percentages of indifferent/spent and active stages of gonadal activity of the southern species and the
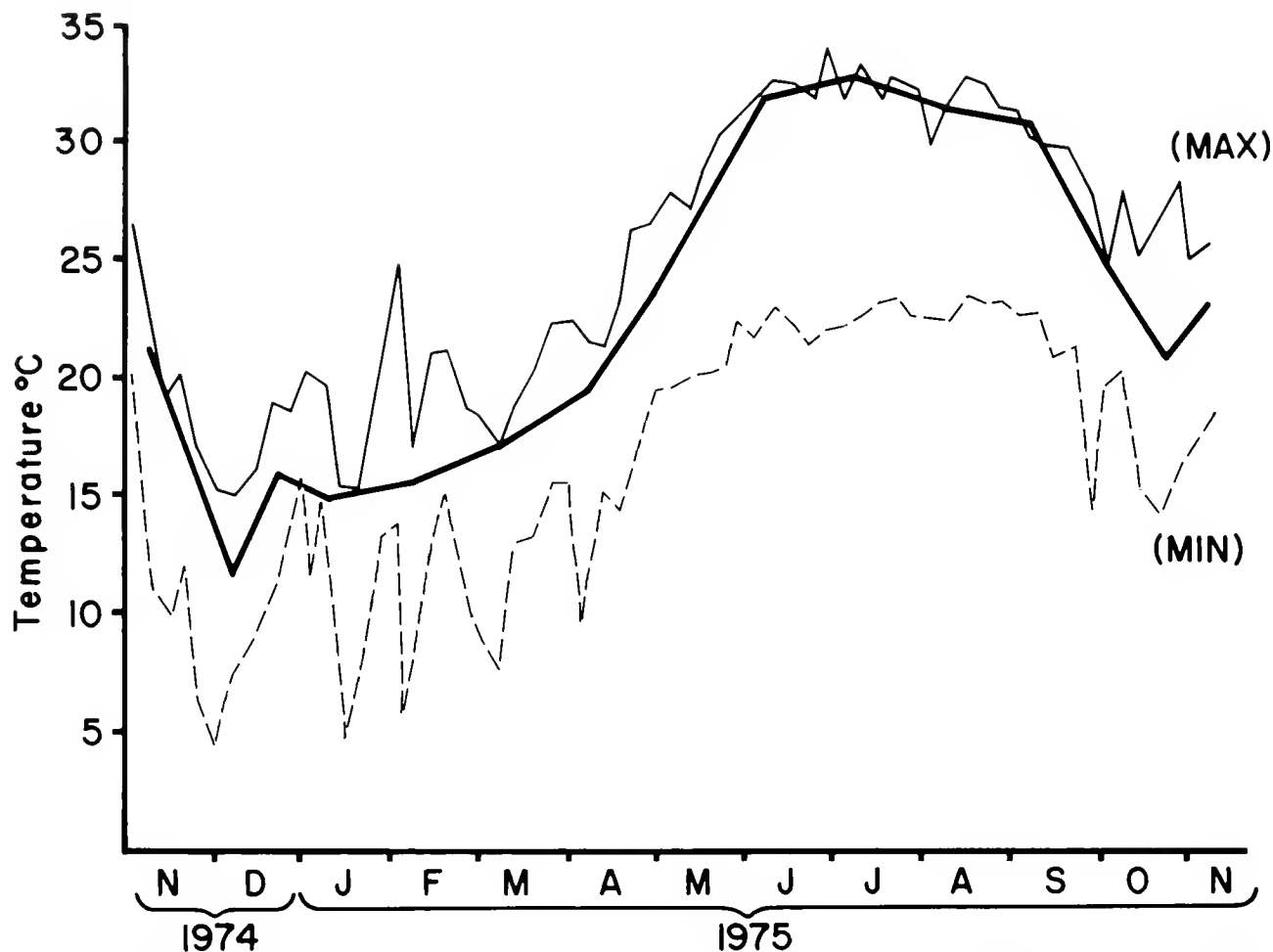
Figure 3. Water temperatures (heavy line) at Alligator Harbor and maximum and minimum air temperatures (mean of 6-day intervals) at Apalachicola, Florida.

hybrid ♀ *Mercenaria campechiensis* × ♂ *Mercenaria mercenaria* were very similar; whereas, the northern and the other hybrid were similar. Menzel (1962) has reported that hybrid quahogs in Florida grew faster than their northern parents and were more like the faster growing southern parent. The hybrid ♀ *M. campechiensis* × ♂ *M. mercenaria* had a slightly better growth rate than the reciprocal hybrid indicating the possibility of maternal influence.

It would be interesting to determine the seasonal gonadal development of females of both species and hybrids in Florida. Previous observations in our laboratory have shown that it is virtually impossible to induce summer spawning of females of any pedigree after about March-April when the ambient water temperatures exceed 22 to 24°C. Active sperm appear in suspensions but few ripe ova occur in clams during the warmer months. Successful female spawnings have been induced during periods from October-March with

no temperature conditioning. The seasonal gonadal development, therefore, may be different for female quahogs than reported here for young males.

Also, it would be interesting to determine if quahogs of both species follow the pattern of gametogensis of the endemic population when transplanted to a colder latitude. Such observations might be difficult because the southern quahog and the hybrids lack a tolerance to low temperatures (Chestnut et al. 1956, Haven and Andrews 1956, Menzel 1977). Whether the northern quahog, native to warmer areas, would survive in cold winter regions is not known. Belding (1912) reported 70 years ago that temperature is the controlling factor in quahog spawning. Based on the data of all the investigations, we believe that both species and the hybrids will have generally similar gamete development and spawning, regardless of their origin, within a specific area.

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EXPERIMENTAL PLANTINGS OF JUVENILES OF THE HARD CLAM
MERCENARIA MERCENARIA (LINNÉ) IN THE WATERS OF
LONG ISLAND, NEW YORK[1]

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ABSTRACT   Planting of hatchery-reared seed of the hard clam *Mercenaria mercenaria* is a significant management tool in town-managed shellfisheries of New York. In the present study, seed planting techniques developed elsewhere were tested in New York waters. The objectives were to determine how seed survival was influenced by (1) seed size at the time of planting; (2) the presence, absence, and type of gravel aggregate; (3) the season planted; and (4) site selection. Site characteristics, particularly the types and abundance of predators present, were found to influence the results so strongly that general recommendations cannot be made. Mud crabs (*Neopanope sayi* [Smith]) and whelks (*Busycon carica* [Gmelin] and *B. canaliculatum* [Linné]) were the most damaging predators at the sites tested. Gravel aggregate did not provide adequate protection for planted clams, and the use of large (25-mm) gravel appeared to have a negative impact on seed survival. Survival exceeded 10% only among clams that were at least 20 mm in length at planting; however, mortalities as high as 100% resulted from plantings of such seed (23 mm) at sites having significant populations of whelks.

KEY WORDS: Hard clams, *Mercenaria mercenaria*, seed planting, predation

INTRODUCTION

The hard clam (or northern quahog) *Mercenaria mercenaria* (Linné) is the object of New York's most important shellfishery, accounting in recent years for about 50% of the total value of fishery products landed in the state (McHugh and Ginter 1978). Long Island's Great South Bay is the single most important producer of hard clams in the world. This 24,282-ha (60,000-acre) bay has historically produced about 90% of the New York harvest and 45% of the total United States harvest of hard clams. Since 1977, New York landings of hard clams have declined dramatically. For example, the 1976 reported Great South Bay landings were 24,684 m^3 (700,465 bu), but by 1981, the landings had dropped to 10,758 m^3 (305,287 bu) (National Marine Fisheries Service, Patchogue, NY, unpublished fishery statistics, 1982).

Although stock assessment data are incomplete, declining harvests are perceived by many local fishery managers to represent a real drop in standing stocks (J. Kassner, Town of Brookhaven, NY, and Pieter Van Volkenburgh, NY Dept. Environm. Conserv., Stony Brook, NY, pers. comm.). Local management agencies, primarily the townships, have responded to declining landings by instituting programs intended to supplement natural hard clam reproduction. Among the most popular programs are those that involve the planting of seed clams. Nine Long Island townships, including all three of the townships that border Great South Bay, have carried out some type of seed clam planting program. Their efforts have ranged from trial plantings of a few thousand seed to annual plantings in excess of 1 million seed. Seed are purchased from a commercial hatchery, held in some type of nursery system, and eventually broadcast onto the bay bottom without any protection. Nursery systems used include shore-based raceways and ponds, rafts, and gravel beds. The size of the seed at the time of release to the public fishery generally ranges from about 8 to 25 mm in shell length.

There are no published studies of seed clam plantings in New York waters. In fact, some doubt has been expressed that the seed planting programs can possibly be of sufficient scale to significantly impact the fishery (McHugh 1981). The early work of Haven and Andrews (1957) showed that seed clams require some type of protection to ensure survival. Similarly, Menzel and Sims (1964) reported that seed clams planted in Florida required protection or had to be at least 12 mm in shell length to avoid very heavy predation losses. Castagna (1970) demonstrated that gravel aggregate helped prevent the loss of seed clams. Castagna and Kraeuter (1977) and Kraeuter and Castagna (1977) recommended the use of aggregate as part of a culture system that included baffles and fences. Their work and the work of Menzel et al. (1976) suggested that the use of stone aggregate alone affords planted seed clams some protection from predators. The use of stone aggregate would be particularly attractive for the extensive nursery plots that are required for large public fisheries because of its relative simplicity and low cost; it has been used on a limited basis for that purpose (Jeffrey Kassner, Town of Brookhaven, NY, pers. comm.).

Eldridge et al. (1979) made the following recommendations based on several years of seed clam planting in South Carolina: (1) select a physically suitable habitat, one that

is free, for example, from extreme wave action; (2) cover the planting area with shell or stone aggregate; (3) plant seed clams in the fall when temperatures are 15 to 18°C; (4) plant seed of 12 to 15 mm shell length at a density of 300 m^2; and (5) harvest in the early summer of the second year. The authors pointed out that uncontrolled variables contribute to the uncertainty of such a planting as a private venture; however, they reported approximately 77% annual survival of 16- to 17-mm seed and 95% annual survival of 21- to 22-mm seed planted in this manner. Later work by Whetstone and Eversole (1981) also reinforced the case for fall plantings by demonstrating in laboratory studies that the activity of an important hard clam predator, the common mud crab *Panopeus herbstii* H. Milne-Edwards, was significantly reduced at temperatures below 17°C.

The present study was part of an effort to test and refine a number of seed-clam planting techniques that have been developed elsewhere. The intention was to evaluate recommended planting procedures for possible application to a large public clam fishery. Specifically, the objectives were to determine in New York waters how the survival of three sizes of planted seed clams was affected: (1) by the size and shape of aggregate and sand substrate (Experiment I); (2) by the time (season) they were planted and recovered (Experiment II); and, (3) by site specific environmental differences within the same general location (Experiment III).

MATERIALS AND METHODS

Experiment I was sited in a shallow cove, separated by a sand spit from Eastern Shinnecock Bay, Long Island, NY (designated as Site 1, Figure 1). Mean low water depth at the site was approximately 0.5 m, and the tidal range averaged about 1.0 m. Sediments within the cove graded from coarse sand near the sand bar to soft mud near the northern edge of the cove. Eeel grass (*Zostera marina* Linnaeus) was present, but was relatively sparse through most of the planting area. A natural population of adults of *Mercenaria mercenaria* existed in the cove prior to our planting at a mean density of about 7 clams m^{-2}.

The seven substrates tested in this experiment consisted of sand and two shapes of gravel obtained in three sizes. The two shapes were (1) mechanically produced, crushed gravel having irregular shapes and jagged edges, and (2) more rounded, unbroken glacial gravel. Both gravel types were obtained in three nominal sizes: 6 to 10, 10 to 19, and 19 to 32 mm. The gravel was washed through wire screens to obtain the approximate size ranges given above. All gravel was obtained from Long Island glacial till and was washed thoroughly with fresh water during processing.

Forty-two plastic, food-handling trays (Nestier® "Chill-tray 180") measuring 56.5 × 46.4 × 17.8 cm were lined with 2-mm mesh plastic window screen. The trays were filled to a depth of approximately 8 cm with 20-mm gravel. They were then transported to the site, arranged in a 6 × 7 array, and hydraulically sunk (jetted) into the bottom so that approximately 3 cm of the tray edges protruded above the substrate. A 4-cm layer of one of the seven types of substrate was then added to the surface of each tray in a randomly generated pattern.

Three sizes of seed clams used in the experimental plantings were obtained from Aquaculture Research Corp., Dennis, MA. At the time of planting (23 July 1980), the mean shell lengths and standard errors (n = 50) for clams of the size groups were 3.9 ± 0.06, 6.8 ± 0.08, and 28.7 ± 0.23 mm. Planting densities used were 1,241, 477, and 191 m^{-2} for the small, medium, and large seed, respectively. Thus, a tray randomly received 325 small, 125 medium, or 50 large seed. The experimental design included two replicate plantings for each treatment. Because there was no differentiation of substrate shape for plantings in sand, for each clam size there were four replicate plantings in sand. Also, because they were in short supply, the largest seed clams were only planted in the three sizes of round gravel and in sand.

The planting area was examined weekly to identify and count potential clam predators. The experiment was terminated on 20–22 October, when water temperatures in the area dropped below 10°C. The trays were lifted on board a small boat, and all remaining clams were removed and counted and their shell lengths were measured to the nearest millimeter. Empty shells and shell fragments were examined for evidence of predation, and any predators recovered with the trays were identified and counted.

Growth and survival (recovery) data were statistically analyzed by analysis of variance (ANOVA) following Sokal and Rohlf (1969). Shell length measurements were used to calculate growth in millimeters.

Experiment II was initiated in the fall of 1980 at two locations (designated Sites IIA and IIB, Figure 1) in Eastern Long Island. Site IIA was located in Shinnecock Bay approximately 30 m east of the previously described site of Experiment I. Site IIA had a mean low water depth of approximately 0.35 m, and bare sandy sediments. Site IIB was located in Napeague Harbor, Long Island. Mean low water depth at the site was 1.0 m, and the tidal range was 0.9 m. Sediment at Site IIB consisted of a 3-cm-deep layer of sand over gravel and stones. The area was devoid of eel grass and macroalgal detritus. A sparse (< 1 m^{-2}) natural population of very large hard clams existed at Site IIB prior to our planting.

Experiment II consisted of two replicate plantings of each of three clam sizes in two substrates types (sand and 1 cm crushed gravel) at two sites and at two planting times. The two planting times and ambient water temperatures at the two sites were: 30 September 1980 (19°C) and 25 November (8°C) for Site IIA, and 30 September 1980 (17°C) and 22 November 1980 (8°C) for Site IIB. Seed clams were again purchased from Aquaculture Research Corp. Mean shell lengths and standard errors (n = 50) for the three size
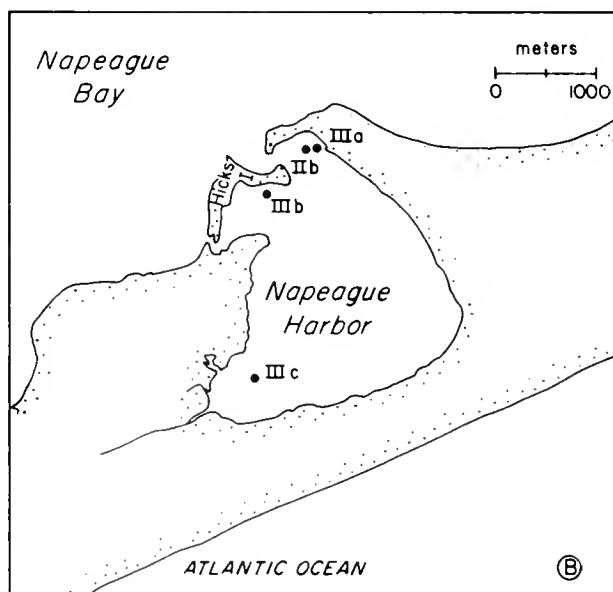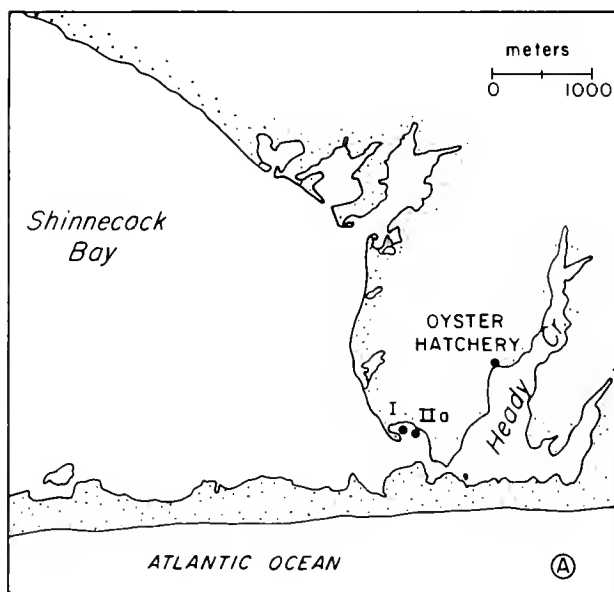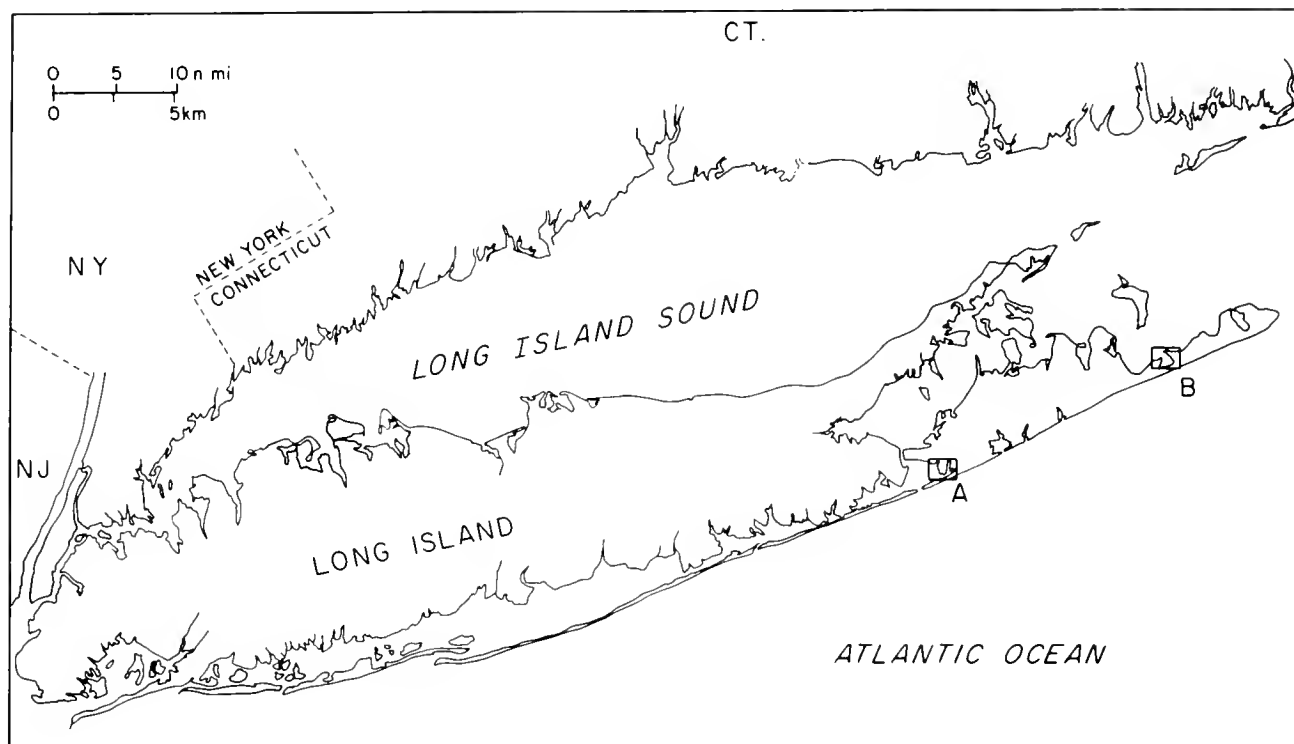
Figure 1. Location of six sites used for experimental plantings of seed clams on the south shore of Long Island, New York.

classes in the September planting were 2.8 ± 0.17, 7.1 ± 0.10, and 22.7 ± 0.15 mm. Rapidly declining ambient water temperatures necessitated the planting of the November shipment immediately upon receipt. Therefore, although hatchery sorting through sieves was identical for the two shipments, shell measurements for the November shipment were not recorded. Tray handling, seed-planting procedures, and planting densities were as in Experiment 1.

The planting sites were inspected regularly for predator distribution and abundance. Final sampling of the trays was conducted 9 months after the planting date (15−22 June and 23−27 August 1981 for the September and November plantings, respectively). Sampling procedures and data analysis were as in Experiment I except that no growth analyses were included in Experiment II.

Experiment III consisted of plantings on prepared natural bottom without trays. Plantings were carried out at three sites (designated as Sites IIIA, IIIB, and IIIC, Figure 1) in one general location, Napeague Harbor, Long Island. Three sizes of seed clams (nominally, 3, 6, and 23 mm in length) were planted at each site, with and without gravel, during the summer of 1981.

Site IIIA was located approximately 40 m east of Site IIB, described above. The site had a mean low water depth of 1.2 m and a tidal range of 0.9 m, and contained poorly sorted sand and gravel sediments.

Site IIIB, in northeastern Napeague Harbor, had a mean low water depth of 0.4 m and a tidal range of 0.9 m. Sediments at the site consisted of coarse sand sparsely interspersed with rocks. The site was on the edge of an approximately 1 ha bare area in an eel grass flat. A dense (20 to 50 m^{-2}) population of small adult hard clams existed at the site prior to our planting.

Site IIIC was located on a large bare sand/mud flat in the southwestern part of the harbor. Mean low water depth was 0.4 m and tidal range was 0.9 m. Hard clams, predominately adults plus a few subadults, were moderately abundant (5 to 10 m^{-2}) prior to our planting.

Seed clams were purchased from the same commercial source in the same three nominal sizes as used in the previously described experiments (2 to 4, 6 to 8, and 22 to 28 mm length). Each of the three sites consisted of six 2- × 2-m subsites delineated by 30- wide × 15-cm-deep borders of 3-cm gravel. Each of the three seed clam sizes were randomly assigned to two subsites. One of the two subsites contained existing substrate, while the other contained a 2.5-cm-deep layer of 1.0 cm gravel. On 20 May 1981, clams were planted at all sites at densities of 1,250, 675, and 260 m^{-2} for small, medium, and large clams, respectively.

Surveys of predator abundance were conducted prior to planting (17−20 May 1981) and were repeated on 26−28 July and 13−14 September 1981. Sampling areas adjacent to each site (30 m^2 in May and July and 15 m^2 in September) were raked with a clam rake lined with 1.3-cm Vexar®,

and predators were collected, counted, and measured. Estimates of the abundance of the more mobile crabs (primarily *Ovalipes ocellatus* [Herbst]) were subject to error because of the animals' mobility and are, therefore, not quantitative.

Sampling to determine seed clam survival was conducted approximately two months after planting (26 July) and again at termination (14 September). For purposes of sampling, each subsite was divided into four 1 m^2 quadrats and each quadrat into nine equal parts (0.11 m^2 each). Two of the 0.11 m^2 areas were randomly selected from each of two randomly selected quadrats. A 0.10 m^2 sampling square was placed on a selected area, and substrate was removed to a depth of 15 cm. After being separated from the substrate, surviving clams were counted and returned to the sample area. Analysis of survival data was as described above.

<div align="center">RESULTS</div>

Experiment I

The most abundant clam predators observed in and around the trays following planting were Say's mud crabs (*Neopanope sayi*), calico crabs (*Ovalipes ocellatus*), channeled whelks (*Busycon canaliculatum*), and oyster drills (*Urosalpinx cinerea* [Say] and *Eupleura caudata* [Say]. Other potential predators which were less frequently observed included blue crabs (*Callinectes sapidus* Rathbun), common mud crabs (*Panopeus herbstii*), and both winter and summer flounders (*Pseudopleuronectes americans* [Walbaum] and *Paralichthys dentatus* [Linnaeus]), respectively.

The abundance of the mud crab *N. sayi* was positively related to increased gravel size (Table 1). Those trays filled with 19- to 32-mm gravel contained numerous 0-year-class crabs. Up to 10 oyster drills (*U. cinerea* and *E. caudata*) per tray occurred during the summer, but no drills were found in the trays during the autumn sampling. Similarly, channeled whelks (*B. canaliculatum*) were visible at the substrate surface, and were most abundant during the first month (August) following planting. Few were observed later in the summer, and only two were recovered from the trays during sampling.

Survival (recovery) of planted seed clams was significantly influenced by their size at the time of planting (0.01 ≥ P > 0.001). Mean survival rates for small, medium, and large clams were 4.0, 43.1, and 82.5%, respectively. The size of the gravel used also significantly affected clam survival (0.01 ≥ P > 0.001). Further, the relationship between grain size, independent of shape, and clam survival appeared to be related to clam size (the interaction was significant; P < 0.01). The smallest seed clams planted (4 mm) did not survive well under any conditions. On the other hand, the survival of the 29-mm seed was high and was independent of grain size. The influence of grain size on clam survival at this site was most evident among the 8-mm seed, which showed declining survival with increased grain size (Table 1).

The shape of the gravel used had no significant effect (P > 0.05) on clam survival.

TABLE 1.

Experiment 1, percent recovery (22 August – 22 October 1980) of three sizes of seed clams planted in three sizes of gravel and in sand. Also shown are the total number of mud crabs (*Neopanope sayi*) recovered from trays containing the four substrate types.

Length of Seed at Planting	Substrate Type				
	Sand	6 to 10-mm Gravel	10 to 19-mm Gravel	19 to 32-mm Gravel	Mean
3.9 mm (n = 4)	14.6	1.1	0.7	0.0	4.0
7.9 mm (n = 4)	68.4	49.6	48.6	5.8	43.1
28.8 mm	77.0	84.0	84.0	86.0	82.5
Total crabs recovered (n = 10)	24.0	36.0	95.0	> 306	

Only a few shell fragments, indicative of crab predation, were found in the trays containing 4-mm seed. The shells of these clams were thin enough to be crushed and consumed by feeding crabs (Landers 1954; Whetstone and Eversole 1978, 1981). Many shell fragments were found in the trays containing the 8-mm seed. Laboratory studies indicated that clams of this size can be crushed and consumed by adult mud crabs, *N. sayi* (Landers 1954, Whetstone and Eversole 1978). Shells of dead clams of the larger (29-mm) seed were primarily paired, intact valves. Several shells had been cracked, possibly by a large calico crab (O. ocellatus) or blue crab (*C. sapidus*). A few shells had chipped or rasped shell margins suggesting predation by whelks, *Busycon* spp. (Carriker 1951, Peterson 1982).

Oyster toadfish (*Opsanus tau* [Linnaeus]) were observed burrowed along the outside edges of three of the trays throughout the summer and autumn. Three of the four trays of 4-mm clams planted in sand had survival rates of 3.0, 2.4, and 5.0%. The fourth tray, next to which a toadfish was burrowed, had a survival rate of 47.3%. Similarly, three of the four trays of 8-mm clams planted in 10- to 19-mm gravel contained a mean of seven mud crabs per tray and had clam survival rates of 48.0, 38.4, and 23.2%. The fourth tray, which had a toadfish beside it, contained no mud crabs and had a survival rate of 84.0%. A third toadfish was found beside a tray containing 29-mm clams. No mud crabs were found in this tray, but clam survival in that tray (82%) was not appreciably different from the mean for clams of that size (82.5%). From these observations, we hypothesize that the toadfish reduced the abundance of mud crabs and enhanced the survival of those seed sizes that were susceptible to mud-crab predation.

Final mean shell lengths for the three clam sizes are given in Table 2. Effects of substrate size or shape on clam growth were not significant for 29-mm seed (P > 0.05). High mortality precluded an analysis of growth in the 4-mm clams. Increasing substrate size did have a significant negative effect on the growth of 8-mm seed ($0.01 \geqslant P > 0.001$).

TABLE 2.

Experiment 1, final mean shell lengths (mm) with 95% confidence intervals (n = 12, time = 85 days) for two sizes of seed clams planted in four types of substrate

Length of Seed at Planting	Substrate Type			
	Sand	6 to 10-mm Gravel	10 to 19-mm Gravel	19 to 32-mm Gravel
3.9 mm	*	*	*	*
7.9 mm	15.4 ± 2.03	14.0 ± 2.21	12.9 ± 2.08	9.5 ± 3.84
28.8 mm	31.8 ± 1.10	33.4 ± 3.05	33.0 ± 0.12	31.7 ± 1.48

*Survival was too low to calculate growth rates.

Experiment II

Predators observed at Site IIA were essentially the same as those listed earlier for nearby Site I. The most abundant predators observed at Site IIB included calico crabs (*Ovalipes ocellatus*) and small knobbed whelks (*Busycon carica*). Mud crabs (*Neopanope sayi*) and small winter flounders (*Pseudopleuronectes americanus*) were present but not abundant.

Significant interactions among the variables tested (size of seed planted, location, time of planting, and substrate type) indicated that unqualified general statements about any single variable cannot be valid (Tables 3 and 4); however, by considering some of the variables together, some important results may be noted. All of the variables tested had significant effects on survival (Table 4). Larger seed showed better survival than small seed, particularly at Site IIA. The September-to-June period resulted in better overall survival than the November-to-August period. Gravel was generally a better substrate than sand for the larger clams at Site IIA, but it did not appear to provide significant survival advantage at Site IIB (Table 3). As in Experiment I, mud crab colonization was greater in gravel than in sand.

Experiment III

Dominant predators observed during Experiment III included small (70- to 80-mm length) knobbed whelks (*Busycon carica*), adult (15- to 25-mm carapace width) mud crabs (*Neopanope sayi*), and adult (45-mm carapace width) calico crabs (*Ovalipes ocellatus*). Abundances of the two major predator species (*B. carica* and *N. sayi*) for which reliable counts could be made at Sites IIIA, IIIB, and IIIC are given in Table 5 for three observation dates.

TABLE 3.

Experiment II, percent recovery (time = 9 months) of three sizes of seed clams in replicate plantings
at two sites in two types of substrate and at two times of the year.

| | | September Planting | | | | November Planting | | | |
| | | Site IIA | | Site IIB | | Site IIA | | Site IIB | |
Clam Size		Sand	Gravel	Sand	Gravel	Sand	Gravel	Sand	Gravel
3 mm		3.6	0.6	0.0	0.3	0.0	0.0	0.0	0.0
		5.7	0.9	0.0	0.0	0.0	0.0	0.0	0.0
	Mean	4.7	0.8	0.0	0.2	0.0	0.0	0.0	0.0
7 mm		6.4	30.4	0.8	4.0	0.0	8.8	0.0	2.4
		11.2	16.0	2.4	1.6	0.8	4.8	0.0	0.0
	Mean	8.8	23.2	1.6	2.8	0.4	6.8	0.0	1.2
23 mm		68.0	94.0	24.0	48.0	48.0	50.0	10.0	18.0
		68.0	96.0	20.0	42.0	34.0	66.0	26.0	14.0
	Mean	68.0	95.0	22.0	45.0	41.0	58.0	18.0	16.0

TABLE 4.

Experiment II, four-way analysis of variance (ANOVA) of
percent survival of three sizes of seed clams (3, 6, and
23 mm) planted in two types of substrate (sand and
gravel) at two locations and at two times of the
year (September and November).

Source of Variation	Mean Square	d.f.	F Ratio
A = substrate type	377.78	1	27.61*
B = clam size	7,140.01	2	521.76*
C = time of year	1,241.96	1	90.75*
D = location	2,244.07	1	163.99*
A × B	187.18	2	13.68*
A × C	33.60	1	2.46 n.s.
A × D	48.72	1	3.56 n.s.
B × C	148.21	2	10.83*
B × D	490.22	2	35.82*
C × D	217.00	1	15.86*
A × B × C	75.60	2	5.52†
A × B × D	69.87	2	5.11*
A × C × D	7.19	1	0.53 n.s.
B × C × D	4.00	2	0.29 n.s.
A × B × C × D	3.93	2	0.29 n.s.
Within	13.68	24	
Total		47	

*significant at 0.01
†significant at 0.05
n.s. = not significant
B > D > C > A

TABLE 5.

Experiment III, abundance of predators (m^{-2}) of the two
numerically dominant predator species, the mud crab
Neopanope sayi and the knobbed whelk
Busycon carica.

| | *Neopanope sayi* | | | *Busycon carica* | | |
| | Site | | | Site | | |
Sampling Date	IIIA	IIIB	IIIC	IIIA	IIIB	IIIC
20 May 1981	2.0	0.3	0.0	2.5	1.0	0.3
28 July 1981	2.0	0.0	0.0	7.0	2.0	8.6
14 September 1981	1.0	0.0	0.0	1.5	1.1	1.2
Mean	1.7	0.1	0.0	3.7	1.4	3.4

In general, survival at Site IIIA was inversely related to
seed size (Table 6). Overall survival was less than 2% even
under the best conditions (3-mm seed in gravel). Only one
of the 6- to 8-mm clams was recovered in July, and by the
termination date (30 September) no clams of that initial
size had survived. No larger seed clams were recovered in
the July sampling. Within a week of planting, empty shells
appeared on the substrate surface.

Maximum recovery of the 2- to 4-mm seed (in gravel)
was 2.2% at Site IIIB. None of the 6- to 8-mm clams was
recovered, and crushed and cracked shells appeared in the
plots within two weeks of planting. Survival of seed planted
at Site IIIB exceeded 50% only among the 22- to 28-mm seed
clams. Note also in Table 6 that among the 22- to 28-mm
seed there appeared to an initial survival advantage to clams
planted in gravel compared to natural bottom, but by the
time of the final sampling in September, survival rates were
very similar in the two substrate types. Chipped shell
margins and cracked shells indicated predation by whelks
and crabs.

At Site IIIC, survival of the small seed in sand, although
still quite low, was somewhat better than that of the larger
seed sizes (Table 6). By the end of the experiment none of

TABLE 6.

Experiment III, percent recovery of three sizes of seed clams planted at three sites in two types of substrates.
Clams were planted 20 May 1981.

Sampling Date	3 mm						7 mm						23 mm					
	Site						Site						Site					
	IIIA		IIIB		IIIC		IIIA		IIIB		IIIC		IIIA		IIIB		IIIC	
	Sand	Gravel	Sand	Gravel	Sand	Gravel	Sand	Gravel	Sand	Gravel	Sand	Gravel	Sand	Gravel	Sand	Gravel	Sand	Gravel
28 Jul 81	3.6	11.0	2.0	3.3	10.4	4.5	0.0	0.0	0.0	0.0	0.0	15.0	0.0	0.0	62.0	88.0	1.7	14.8
14 Sep 81	1.5	1.8	1.2	2.2	6.2	4.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	58.0	61.0	0.0	5.3

the 6- to 8-mm clams remained, and a few 23-mm seed survived only in gravel (5.3%). Heavy losses of the larger seed clams, the chipped or rasped shell margins of articulated, empty valves remaining in the planting areas, as well as the high densities of knobbed whelks (*B. carica*) at this site (Table 5) suggested that predation by whelks was an important cause of mortality.

DISCUSSION

The results of this study demonstrated that the characteristics of a given site, especially the types of predators present, had an important influence on the loss and presumed mortality of planted seed clams and on the degree of protection afforded by recommended culture techniques. For example, we found that at sites such as Site IIIA where whelks (*Busycon canaliculatum* and *B. carica*) were abundant, plantings of 25-mm seed clams suffered complete mortality despite the presence of gravel aggregate. At sites such as Site IIIB where mud crabs (*Neopanope sayi*) were the dominant predator, the smallest seed clams suffered high mortality, while the larger seed showed good survival. Clearly, the idea that seed clams having at least a 25-mm shell length are relatively immune from most predators (Menzel 1971, Eldridge et al. 1979) is valid only when the seed is planted at sites lacking significant populations of large predators. Existing literature has convincingly shown that the activity of some important predators such as mud crabs is significantly reduced by lower autumn temperatures (Whetstone and Eversole 1981); however, we found that autumn plantings eventually suffered the same high mortalities as the summer plantings, and the choice of planting season was inadequate protection against crab predation.

The use of gravel aggregate at Site I, where the mud crab *N. sayi* was the dominant predator, gave inconsistent results in our Experiment I (Table 1). At that site, mortality among the smaller clams was complete and was independent of the presence or absence of gravel. On the other hand, mortality among the larger clams was very low, but it was again independent of substrate grain size. The survival of the medium size (7.9-mm) seed was inversely related to gravel size. The 6- to 10-, 10- to 19-, and 19- to 32-mm

gravels, all of which are within the size range (10 to 30 mm) used by Castagna and Kraeuter (1977), were not consistently effective in enhancing seed clam survival (Table 1). Densities of the mud crab *N. sayi* were much higher in gravel beds than in the bare sand (Table 1). There is also evidence from our data (Table 2) of reduced growth rates among small seed clams planted in larger gravel compared to those planted in sand or small gravel.

Gravel may be useful in preventing small clams from being carried away by currents, although our work offers no direct evidence for this. It is also possible that gravel and shell substrates offer more effective protection against larger crab species than against relatively smaller species such as *N. sayi*. Size-related differences in the food and space utilization of two sympatric xanthid crab species (*Panopeus herbstii* and *Eurypanopeus depressus* [Smith]) were discussed by McDonald (1982). He noted that the larger of the two species (*P. herbstii*) was prevented by its size from entering narrow spaces between living oysters. This suggests that the lack of consistent results from seed plantings in gravel might be due in part to site-specific differences in the relative abundance of large and small crabs.

Previous studies have shown that xanthid mud crabs (primarily *N. sayi*) are the most abundant clam predators in Long Island's Great South Bay (MacKenzie 1977). Their mean, baywide abundance is about 4.4 crabs m^{-2}, while that of *Ovalipes ocellatus* is about 0.2 crab m^{-2} (WAPORA, Inc. 1981). Mud crabs are capable of consuming 1.6 to 5 small (5- to 10-mm) hard clams each day (Landers 1954, MacKenzie 1977). Theoretically, mud crabs in Great South Bay could consume up to about 20 seed clams m^{-2} day^{-1}. At this rate of loss, seed plantings of 200 to 500 clams m^{-2} would not survive long. Consequently, local seed planting efforts that do not somehow protect the young clams until they are large enough to avoid mud crab predation will probably be unsuccessful.

Although seed hard clams are readily available from commercial hatcheries, their cost is relatively high. Costs for 3- to 5-mm seed range from $10 to $15/1,000 at the present time (J. Kassner, Town of Brookhaven, NY and

S. Buckner, Town of Islip, NY, pers. comm.). Assuming that harvested littleneck clams have a dockside value of about $70 per bag of 500, then the survival and harvest of planted seed (initially costing $12/1,000) must exceed 9% of the number planted for the value of the harvest to exceed the cost of the seed alone. A typical Long Island town program might plant about 2 million seed and could require about 6 man-months of handling and planting time. If the costs of handling and planting are added to the cost of the seed itself, then the survival requirement might increase to about 15%. This estimated survival requirement is relatively low compared to other estimates for commercial culture (40% by Castagna and Kraeuter 1977, 50% by Menzel et al. 1976). It should be remembered that our estimated survival and harvest requirements are minimum values for seed planted in a public fishery. Existing programs involve relatively little handling and no maintenance or protection after planting on the bay bottom. If the costs of a nursery system (rafts, racks, etc.) were added to our estimate, the survival requirement for cost effectiveness would approach those given above for commercial systems.

Our essentially unprotected plantings of 3- to 5-mm seed clams rarely resulted in survival rates as high as 10%, even in short-term experiments. Other work, summarized in Table 7, showed similar results with seed of this size. In fact, 0% survival was the most commonly encountered result of unprotected planting of small seed clams. Even when various types of protective measures were employed, mortality among small seed clams often exceeded 50% (Table 7).

The relatively low expected survival rates contribute to the problem of scale in these programs (discussed by McHugh, 1981). For example, a survival rate of even 15% would leave only 300,000 clams available for harvest from a planting of 2 million seed. In the very unlikely event that all of these clams were harvested, this would yield only 21 m^3 (600 bu), or about 0.6% of each of the three Great South Bay towns' typical annual harvest. In fact, available data (Table 7) indicate that survival rates and consequential harvest contributions might be much lower.

TABLE 7.

Published accounts of some trial plantings of seed clams (*Mercenaria mercenaria*) on the Atlantic coast of the United States.

Reference	Seed Size Planted (mm)	Seed Size Recovered (mm)	Duration (Months)	Approximate Survival (%)	Notes
Menzel and Sims (1964)	33–44	–	–	82–95	Protection (fence, baited traps)
	33–44	–	–	0	No protection
Godwin (1968)	18–22	–	10	0	No protection
	18–22	35–37	10	50	No protection
	18–22	–	10	0	No protection
	18–22	50–52	10	51	Protection (wire mesh)
	18–22	36–37	10	36	Protection (wire mesh; loss due to "winter-kill")
Menzel (1971)	15–35	–	–	90	Protection (fence, traps)
Walne (1974)	9–13	17–21	6	88	Protection (plastic mesh)
Eldridge et al. (1976)	12–13	16–25	4	64	Protection (covered trays)
	16–25	29–45	12	76	Protection (covered trays)
Menzel et al. (1976)	7–10	–	11	0.6	No protection
	7–10	–	11	2.3	Protection (shell cover)
	7–10	–	11	10.1	Protection (gravel)
	7–10	–	11	58.6	Protection (wire mesh)
Eldridge et al. (1979)	13	16–19	4	62	Protection (covered trays)
	16–19	46–57	24	81	Protection (same planting as above)
Castagna and Kraeuter (1977)	2	–	11	75	Protection (gravel, traps, baffles)
Kraeuter and Castagna (1977)	2	–	11	0	No protection
	2	17	11	1– 3	Protection (gravel only)
	2	17	11	10–22	Protection (gravel, baffles)
Kraeuter and Castagna (1980)	32	39	4	94	Protection (pen, gravel, baffles)
	32	39	4	9	Protection (no pen, with gravel, baffles)

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TRANSPORT OF BIVALVE LARVAE IN JAMES RIVER, VIRGINIA[1]

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ABSTRACT   For nearly 100 years, the James River has been the primary source of seed oysters for Virginia. A disease caused by *Minchinia nelsoni* (MSX) killed most oysters in high-salinity waters in the lower river in 1959 and 1960, and planting has not been resumed in these areas (Andrews 1983). Large populations of oysters on Hampton Bar and near the mouth of the river which served as broodstocks were destroyed. After 1960, setting declined drastically in regularity and intensity to about one tenth of that which occurred in the 1950's. Setting patterns suggest two types of seed areas in Chesapeake Bay: (1) high freshwater discharge, open or flushing estuaries with light spatfalls that decrease in intensity with distance from the river mouth; the James River is a typical example; and (2) low discharge, trap-type estuaries where intensive sets are heaviest near the head of the saline sector; examples are the Piankatank and Great Wicomico rivers in Virginia. Larval transport systems in the two estuarine types differ in quantity of larvae retained and regularity of spatfalls. Hourly plankton samples in the James River during 10 days in 1964 and 1965 revealed regular cyclic abundance of larvae with tidal stages. Larvae were 5 to 10 times more numerous during high-tide periods than at low-tide periods. Mostly early-stage larvae were distributed randomly throughout vertical columns of water. Larvae of other bivalve species exhibited similar distributions and fluctuations in abundance with tidal stages. Patterns of larval distribution were similar for all depths at five stations, both in the channel and over oyster beds, during 16 tidal cycles in 1965. Frequent recruitment of new larval broods and disappearance of most oyster larvae before ages of 3 to 5 days suggest losses due to physical dispersion and predation. Only when larvae reached advanced umbo stages did they actively select deeper water strata in the channel which provided a transport system to carry them upriver. In the 1950's, spatfall occurred every week in the James River from 1 July to 1 October each year; since 1960, light, erratic setting has prevailed every year. If one assumes that predation, larval ecology, and physical transport systems have not changed, it appears that broodstocks have become inadequate, or that larvae were killed by toxic substances.

KEY WORDS: Molluscs, bivalve larvae, transport, distribution, setting (or spatfall), James River, VA

INTRODUCTION

The James River has supplied seed oyster (*Crassostrea virginica* [Gmelin]) for most private grounds in Chesapeake Bay for over 100 years (Andrews 1951, 1955, 1982a). The seed area is located in low-salinity waters (< 18 ppt in late summer) between the James River Bridge and the Deep Water Shoal (Figure 1). The horizontal salinity gradients in the James River are steep compared to those of other estuaries in Chesapeake Bay; salinity in the upper river seed beds ranges from 0 ppt in late winter and spring to 10 or 12 ppt in late summer and fall. Consistent annual spatfalls of moderate intensity averaged 2.7 surviving spat per shell over 17 years from 1944 to 1960 (Andrews 1982a). During that period, 90% of surviving spat set on other oysters. Two to three million bushels (7.0 to 10.6×10^4 M^3) of seed oysters were harvested annually without depleting James River stocks. Oysters in the seed area were stunted in growth and storage of glycogen was low; therefore, they produced small quantities of spawn; but high-density populations were spread over large areas of natural shell beds; no management was applied except for limited harvesting by hand tongs. Good quality seed oysters with many single oysters and small clumps resulted from regular

spatfalls and low survival of initial sets (2 to 4% [Andrews 1949]). Compared to high-salinity areas along the Atlantic coast of North America, those survival rates were high (Mackin 1946).

Two types of seed areas are recognized in Chesapeake Bay based primarily on size of drainage areas and amount of freshwater discharge (Andrews 1979, 1982b). In the category of high-freshwater flow are the Susquehanna, Potomac and James rivers, but only the James permits recruitment of young oysters with enough regularity and intensity to be a seed area. Strong freshwater discharge provides the motive force in these estuaries to establish strong salinity gradients and a net counterflow of salty water upriver in the channel; it also produces high flushing rates to discharge the additional fresh water. The other category of estuaries, which I call trap-type seed areas (Andrews 1979), consists of low-discharge rivers with small drainage areas. Two examples of this type seed area which have been studied are the St. Marys River (Manning and Whaley 1954) for distribution and retention of larvae, and the Manokin River (Carter 1967) for circulation regimes. Other important seed areas in Chesapeake Bay which belong in this trap-type category are the Piankatank and Great Wicomico rivers in Virginia, and Broad Creek, a branch of the Choptank River in Maryland (Boicourt 1982).
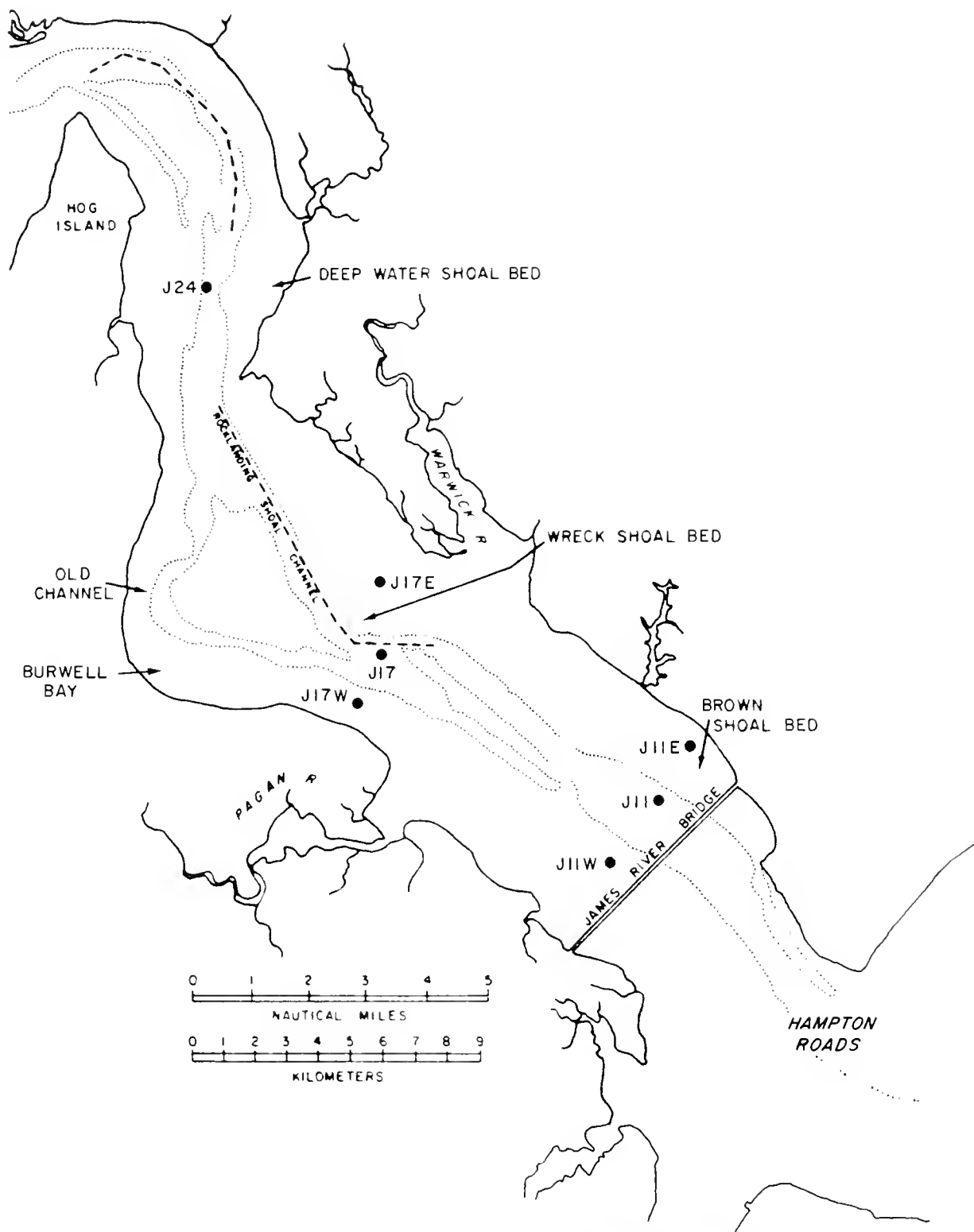

Figure 1. Map of James River seed area from Hampton Roads to last upriver seed bed at Deep Water Shoal. Sampling stations and associated oyster beds are designated in kilometers from mouth of the river.

The oyster setting patterns in these high-flushing and trap-type estuaries reflect differences in circulation patterns that result in dispersion or retention of larvae. The James River is the only flushing-type estuary in Chesapeake Bay with adequate spatfall to be a seed area. Spatfall was consistent annually, but from low to moderate in intensity; it exhibited a gradient of declining setting intensity from the mouth to upriver areas (Andrews 1982a). The gradient of setting was reversed in trap-type estuaries with highest spatfalls on the upriver beds (Manning and Whaley 1954, Andrew's data in Haven et al. 1978). For comparison, setting was consistent in intensity and regular by years in the James River; but intensity was much higher in trap-type estuaries and quite irregular by years with frequent failures. There was no change in the patterns of spatfall in trap-type estuaries following introduction of the disease caused by *Minchinia nelsoni* (MSX) to Chesapeake Bay in 1959 (Andrews and Wood 1967); but in the James River there was a severe reduction in setting intensity and spatfall became erratic in distribution (Haven et al. 1978). All seed areas in Chesapeake Bay are in low-salinity (< 20 ppt) waters and usually not subject to MSX infections and mortalities; broodstocks were greatly reduced in the lower James River by MSX, but they were not in the trap-type seed areas which are located upbay and lay mostly above the endemic area for the disease.

The geography and morphology of the two types of estuaries are probably significant factors with respect to dispersion and retention of larvae (Andrews 1979). The James River has a wide, deep channel, bordered by wide, shallow flats where oyster beds are located; it has few tributaries and limited marsh areas adjacent to the oyster-growing sector. The trap-type seed areas have meandering channels, numerous projecting points, very shallow flats, and many tributary creeks. Reduction and deflection of currents by boundary effects and morphometry in these tortuous estuaries probably aid in retention of larvae. The Great Wicomico River is an excellent example of the morphology of a trap-type estuary with its characteristics of infrequent but intensive spatfalls. Over 30 years, failures have been more frequent than successes in the Virginia trap-type rivers (Haven et al. 1978).

The first study of larval transport in Chesapeake Bay was conducted in the James River in 1950 by the Virginia Fisheries Laboratory and the Chesapeake Bay Institute (CBI) (Pritchard 1953). An intensive study of physical and chemical hydrology was conducted by CBI (Pritchard 1952, 1955). Concurrently, bivalve larvae were sampled bi-hourly by Virginia biologists at three stations across the river at the Wreck Shoal (J17) level (Andrews 1982c). Wreck Shoal is the largest and most productive oyster bed in the James River. The last period of sampling, from 30 August to 3 September, coincided with peak setting of oysters in that year with 40 spat per shellface per week on four replicate shell strings that were suspended off the

bottom at Wreck Shoal (Andrews 1951). Larvae were scarce at all stations and all sampling depths (3 depths in channel, 2 over beds). Primarily, straight-hinge larvae of less than 3 days of age were found, and many samples had no oyster larvae. Advanced larvae were encountered only rarely even when volume of plankton samples was increased from 100 to 500 ℓ (Andrews 1982c). Preliminary data on larval densities were presented by Pritchard (1953) who calculated that only one mature larva per 100 ℓ was needed to produce the observed spatfall. No conclusions were reached about distribution systems for larvae and for their retention in the seed area.

The studies of Manning and Whaley (1954) in St. Marys River, Maryland, a trap-type estuary, were far more conclusive because advanced larvae were abundant and they moved upriver with wind-induced currents. Larvae in all stages were found and often 100 or more late-umbo larvae in 100-ℓ samples. Densities of advanced stage larvae were much higher in deeper waters in the channel with peak counts of 900 late-umbo larvae per 100-ℓ sample. Manning and Whaley concluded that wind-induced convection currents moved surface waters landward in the lower-river sector with downriver flow in bottom layers. The typical characteristics of trap-type seed areas with tortuous geography and most intensive spatfalls near the head of the estuary are illustrated in Figure 1 of Manning and Whaley (1954).

Carter (1967) conducted a physical study of hydrography of Manokin River on the Eastern Shore of Maryland using point release of dye to simulate physical dispersal of larvae. His conclusions were similar to those of Manning and Whaley (1954) that wind-induced convection currents carried larvae upstream. Freshwater discharge was almost negligible as in St. Marys River. Although the Manokin River is not a seed area, it could be according to Carter if enough brood oysters were planted in the lower river. Seliger and Boggs (1983) examined the physical hydrography of the Choptank River and its tributaries; they confirmed the physical regimes of trap-type estuaries but provided little information on larval biology from limited sampling, except that larvae were most abundant at the heads of saline river systems (creeks) where setting is known to be highest (Meritt 1977). More detailed studies of circulation in tributary creeks of the Choptank River were made by Boicourt (1982).

Mechanisms of transport and setting of planktonic larvae in other estuaries are discussed by Ketchum (1954) in general, by Korringa (1952) for oysters in the Oosterschelde (Holland), and by Carriker (1951), Nelson (1957) and Haskin (1964) for oysters in New Jersey coastal bays and Delaware Bay. There is considerable literature on upstream movements of fish and crustaceans (e.g., Sulkin 1981), but larvae and juveniles of these groups make more positive responses to favorable strata and currents than do bivalve larvae. The most important bivalve larval studies of open

systems such as James River are those of Kunkle (1958) and Hidu and Haskin (1971) along the Cape May shore in Delaware Bay. In 1964–1965, mature and eyed-larvae were abundant in 200-ℓ samples collected by the latter authors with 160-μm mesh plankton nets, and setting was intense. This area consistently had intense spatfalls (Nelson 1959), often far higher than any place in Chesapeake Bay. Delaware Bay is similar to James River in physical characteristics, but it has lower freshwater discharge than does Chesapeake Bay (Boicourt 1982). It has a tidal range of nearly 2 m, which is twice that of Chesapeake Bay ($\bar{x}$ = 0.72 m). Tidal- and wind-induced mixing in this wide, shallow bay, as in the James River, prevent much vertical density stratification in summer. By Pritchard's (1955) criteria for circulation regimes, both estuaries are type C in summer with lateral mixing; because of decreased river discharge and wide, shallow basins, salt balance is maintained by circular flow (Pritchard 1956).

This report describes the patterns of larval transport in the James River and compares transport of larvae in the two types of estuaries. During 22 years (1946 to 1967) of intensive monitoring of spatfall in James River, the final distributions of larvae were determined (Andrews 1951, 1955, 1982a), but how they became distributed throughout the seed area is still obscure. The importance of large broodstock populations was shown after 1960, when setting rates declined to less than one-tenth the 1950's level; this followed cessation of private oyster planting in the lower river (Haven et al 1978, Andrews 1982a). High mortalities caused by MSX prohibited use of James River seed oysters in high-salinity waters of the lower river (Andrews 1983). Scarcity of oyster larvae during the 1960's, particularly of advanced stages, made studies of larval ecology difficult. Descriptions of the two types of seed areas are based primarily on patterns of spatfall that indicated wide differences in retention of larvae. Larval studies have not been made in trap-type estuaries in Virginia. Dye studies conducted in a physical model of James River at Vicksburg, Mississippi, suggested the probable extent of larval dispersion if transport were passive (Hargis 1966). Only field data collected in James River when sampling was most intensive in 1964 and 1965 are reported here. Data for earlier larval studies in James River are reported by Andrews (1982c). Some physical data collected during the 8 days of plankton sampling in the 1965 study were reported by Wood and Hargis (1971).

MATERIALS AND METHODS

Scarcity of larvae at Wreck Shoal in 1950 and recognition of higher spatfalls in the lower river resulted in selection of the Brown Shoal area for sampling in 1964 and 1965. Based on intensity of spatfalls over 20 years and preliminary plankton samples each year, a period near 1 September was chosen as the optimum time for sampling. This would not be true of any other estuary in Chesapeake Bay because the

James River always has late setting. More emphasis was placed on sampling in the channel than over inshore oyster beds because deep-water currents are necessary for physical transport upriver. The channel is considered to be the primary transport route for upstream movement of larvae. Sampling was conducted hourly during night and day at four depths (0, 3, 6, 9 m) in the channel and at two depths over 3-m-deep beds for 2 days in 1964 and 8 days in 1965. After finding early-umbo larvae in the channel at Brown Shoal on 31 August 1964, stations were established at J33 in the channel and at Wreck Shoal (J33E) bed where sampling occurred for one tidal cycle on 3 September 1964.

Three vessels were spaced 2 km apart and anchored in the channel in 1965, and two were anchored inshore over oyster beds opposite the central channel station above the James River Bridge. All plankton samples were taken synoptically on the hour with submerged pumps for each depth. Volume of water was measured by timing of calibrated pumps. Samples of about 300 ℓ were pumped into plankton nets with 50-μm mesh submerged in watertight boxes. Surface and bottom samples were taken 1 m from interfaces with air and substrate to avoid boundary effects on currents and larvae.

Plankton samples were preserved with 1% formalin buffered with an excess of $NaHCO_3$ or $NaBrO_3$ crystals. Counts of all species of bivalve larvae were made on Sedgwick-Rafter cells. In 1964, three or more 2-cm^3 aliquots were pipetted from magnetically stirred samples condensed to about 60 cm^3. In 1965, entire samples were counted after excess fluid was decanted; sediments were swirled in 10-cm watch crystals to remove lighter periferal plankton and fecal pellets with pipettes. Several slides were counted for each swirl depending on the amount of sand and sediment; three or more swirls were made for each sample until larval counts declined rapidly. Early- stage larvae are lighter than advanced larvae, therefore they are more difficult to separate from other plankton by this swirling method. Total sample counts were necessary because of low density of larvae. All species were counted separately by stages of development; these were designated as straight-hinge, early-umbo, late-umbo, and mature or setting-size larvae (Chanley and Andrews 1971). Species and stages with low abundance were not summarized except as total bivalve larvae. Oysters comprised about one half of the bivalve larvae in most samples.

RESULTS

Brown Shoals was sampled hourly through one tidal cycle on 31 August 1964. A density of 10 to 40/ℓ of early-stage oyster larvae with some advanced larvae was encountered. A severe thunderstorm interrupted this field study at midnight, but a new operation during one daytime tidal cycle was carried out at J19 and J33 on 3 September 1964. Counts of total bivalve larvae in the channel at J19 are shown in Table 1. Bivalve larvae were two to several

times more abundant at 3- and 6-m depths than at 0 and 9 m near surface and bottom boundaries. Larvae at 3 m depth had reached abundances of 30/ℓ at maximum flood tide and stayed high through high-slack water to maximum ebb. It is clear, however, that larvae were patchy in local distribution at various sampling times. A new group of early-stage larvae, 2 to 3 days old, had entered the Brown Shoal area on 3 September, and advanced larvae were less abundant than they had been on 31 August.

TABLE 1.

Total of bivalve larvae per 10 liters by depths in channel at Brown Shoal (J19), James River, 3 September 1964.[*]

Time	Tide	Bivalve Larvae by Depth (m)			
		0	3	6	9
1000–1100	early flood	15	61	87	--
1100–1200		3	118	228	158
1200–1300		29	387	676	278
1300–1400	maximum flood	17	298	118	54
1400–1500		18	529	163	86
1500–1600		15	483	170	36
1600–1700	high slack	77	424	397	36
1700–1800		111	341	263	124
1800–1900	maximum ebb	189	640	222	168
Mean		47	328	233	105

*70% oyster larvae

Samples at station J33 in the Wreck Shoal area on 3 September 1964 showed that advanced oyster larvae had moved upriver (Table 2). This table is arranged to show increasing densities of advanced-stage larvae with greater depths. Advanced larvae were much less abundant inshore over Wreck Shoal at station J33E in 3 m of water than in the channel. Again, patchiness of larvae was evident although some late-umbo larvae were found at all depths sampled. These counts were made by P. Chanley and the first 50 larvae were measured for size. This was the only one of 17 days sampled during full-tidal cycles over four years (1950, 1963, 1964, 1965) when significant numbers of advanced oyster larvae were found in James River. A light spatfall from these larvae occurred throughout the seed area in two subsequent weeks (Andrews 1982a).

Hourly sampling around the clock from 5 and 3 stationary vessels, respectively, for 8 days (30 August to 3 September and 9 to 11 September) in 1965 showed bivalve larvae in regular cycles of abundance with tidal stages. High abundances occurred from maximal flood velocities through high-slack water to maximal ebb velocities, and low densities occurred during the other half of each tidal cycle. Combined totals for all bivalve larvae for four depths in the channel are shown for two stations (Figure 2). Most larvae of all species, including oyster larvae, were at straight-hinge stage (Andrews 1982c). Data for total bivalve larvae by four depths at one channel station exhibited similar patterns of cyclic abundance (Figure 3). Early-stage larvae were

TABLE 2.

Population densities of advanced oyster larvae (number per liter) by depths in channel at Wreck Shoal (J33), 3 September 1964.

Time	Oyster Larvae by Depths (m) and by Sizes (μm)[1]								
	0			3.5–4.0			7.0–8.0		
	<125	125–200	>200	<125	125–200	>200	<125	125–200	>200
1125							50	17	42
1208	11	0	0						
1227				1877	0	0			
1300	349	32	0						
1325				818	82	0			
1345							412	252	137
1359	429	40	0						
1420				698	63	63			
1442							201	218	84
1500	285	11	0						
1522				550	160	0			
1544							49	86	74
1600	177	48	16						
1624				166	128	0			
1646							0	59	215
1701	406	41	14						
1725				318	49	24			
1743							427	197	66
1800	202	34	0						
Mean	266	29	4	738	80	14	190	138	103

[1] Stages of larvae by size are: straight-hinge = <125 μm; early-umbo = 125 to 200 μm; late-umbo or eyed = >200 μm.
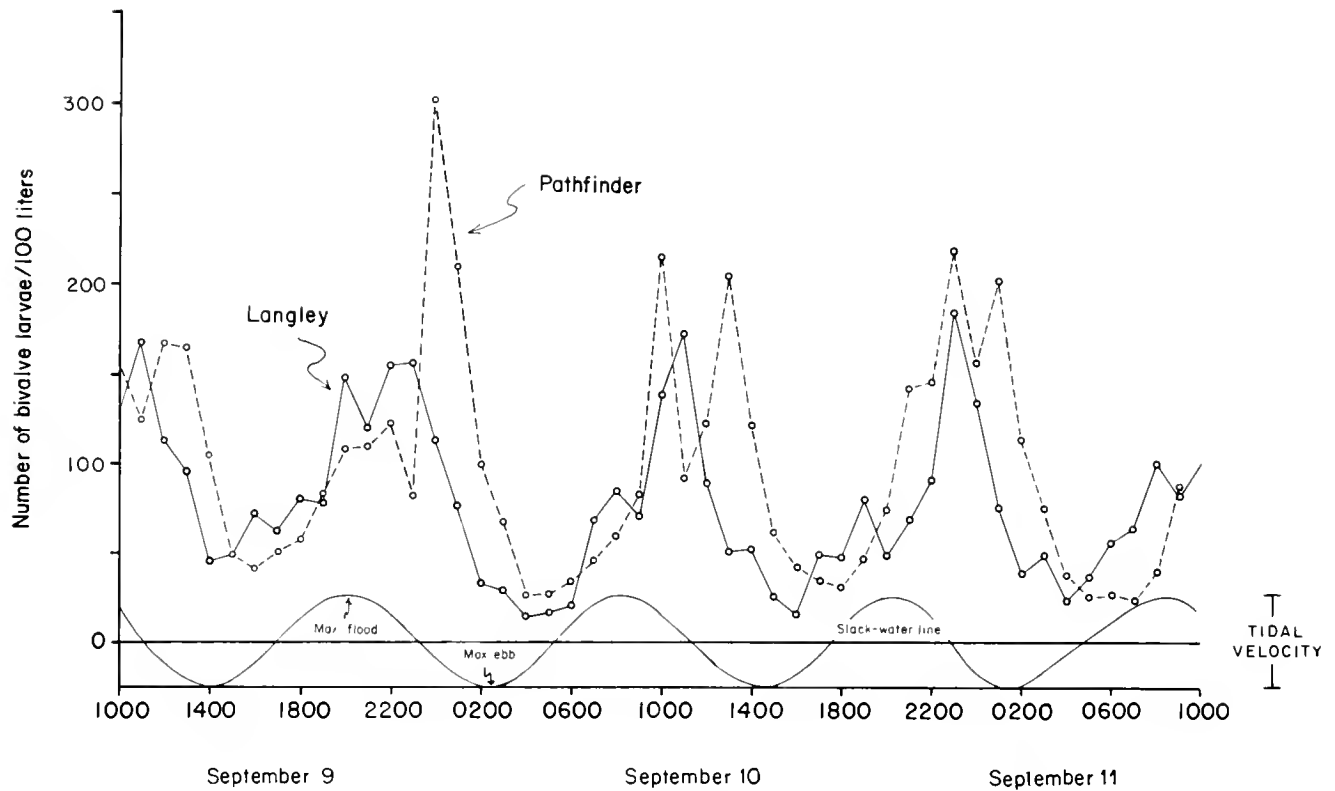
Figure 2. Hourly densities of total bivalve larvae at four combined depths in channel, 9 to 11 September 1965. Two sampling stations designated by anchored vessels R/V LANGLEY and R/V PATHFINDER in channel 2 km apart. Total counts from 300-ℓ samples at four depths adjusted to number per 100 ℓ Similar cycles of abundance occurred each tidal cycle at five stations over a period of 8 days between 30 August and 11 September 1965. Early-stage larvae predominated throughout the period.
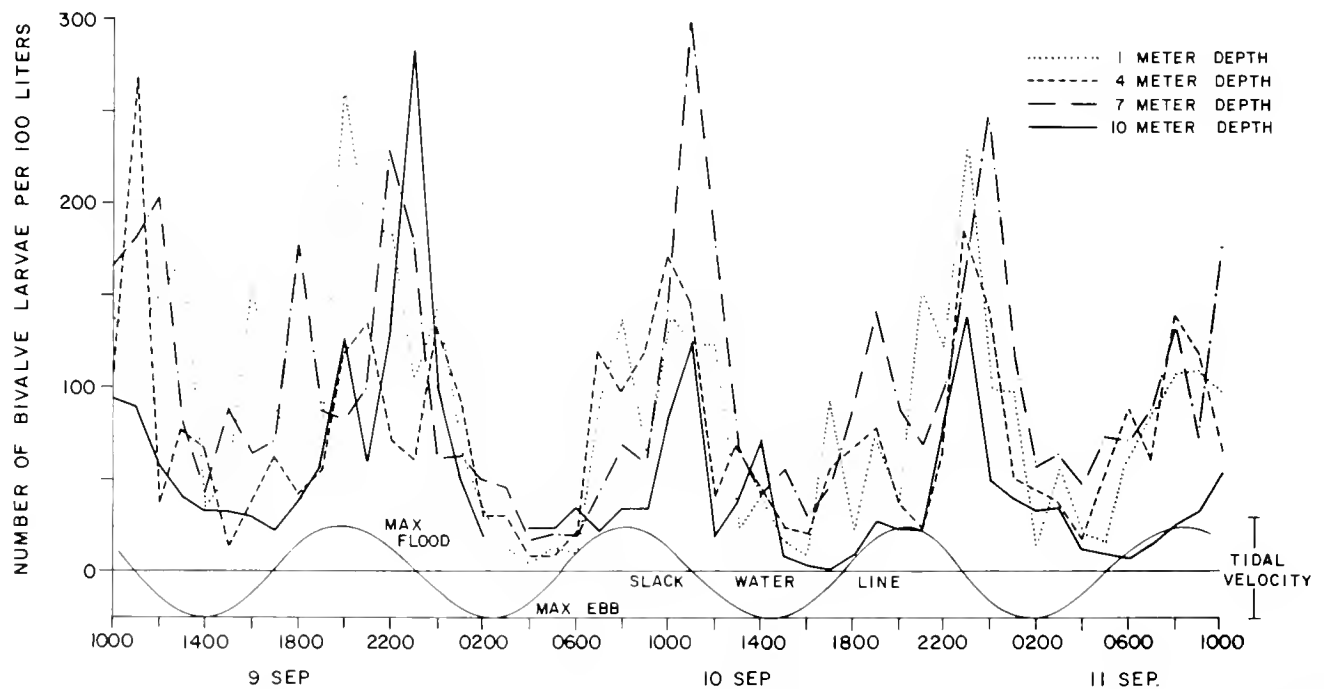

Figure 3. Cyclic abundance of bivalve larvae with tidal stage by depths in channel. Samples taken simultaneously with four submerged pumps at four depths at station J19.

distributed throughout vertical columns of water with highest densities usually at 4 and 7 m.

Data on bivalve larvae by species also showed highest densities from mid-flood to mid-ebb tidal velocities (Figure 4). Patchiness was evident, but peaks of abundance for oysters and other bivalves tended to occur near high-slack-water stage. Highest densities at high tides were 5 to 10 times as great as lowest densities at low tides. Oyster larvae were the most abundant of bivalve species, but peak densities tended to occur concurrently for all species.

The cyclic abundance of larvae in shallow waters (< 3 m) over oyster beds is illustrated in Figure 5. High and low densities appeared at the same tidal stages as in the channel but tended to differ more widely in densities.

DISCUSSION

Oyster spawn is released at least weekly during summer from late June through September in the James River, but spatfall is most successful in late August and early September (Andrews 1955). Although spatfall occurred every week from 1 July to 1 October in the 1950's, 25 years of setting records indicate that conditions for survival and transport of larvae are most favorable in late summer (Andrews 1982a). This is a period of low-freshwater discharge and high salinities; therefore, stratification is minimal and net upriver movement of saline water in the channel at depths below 3 m is small and slow (Pritchard 1953, 1955). Nevertheless, in contrast to trap-type estuaries, the James River always has freshwater discharge which induces some stratification and mixing upriver in the seed area. Hampton

Roads is nearly homogeneous for density of water in late summer, yet some saline water must move upstream in the channel to maintain salt balance in the seed area. Salinities increase gradually in the seed area as summer progresses.

Dye releases near the mouth of the James River in the Vicksburg model showed that a 28.3-m^3/s (1,000-ft^3/s) discharge rate, which approximated salinity regimes observed in late summer of 1964 and 1965, resulted in higher concentrations of dye at Burrells Bay after seven prototype days than a 90-m^3/s (3,200-ft^3/s) discharge (Hargis 1966). This suggests less importance of salt-balance transport upriver and greater effects of high-flushing rates that remove larvae from the river. If tidal dispersion is the primary factor or transport system regulating distribution of bivalve larvae, late-summer hydrographic regimes would be most favorable for retention of larvae in the river.

Oyster larvae originate over shallow inshore flats and oyster beds in the James River. Early-stage larvae occur in the full vertical column of water over flats and in the channel; therefore, most larvae released in the seed area are probably carried downriver in shallow surface waters during their first days of planktonic life. Before MSX stopped the planting of seed oysters in Hampton Roads, a large oyster population near the river mouth supplied large quantities of spawn. In post-MSX years after 1960, most larvae originated in the seed area. The topography of the river below the James River Bridge delivers larvae off the extensive eastern shore seed beds into the channel of Hampton Roads where a deep-water column of 10 m or more is thoroughly mixed and available to allow vertical redistribution of larvae for
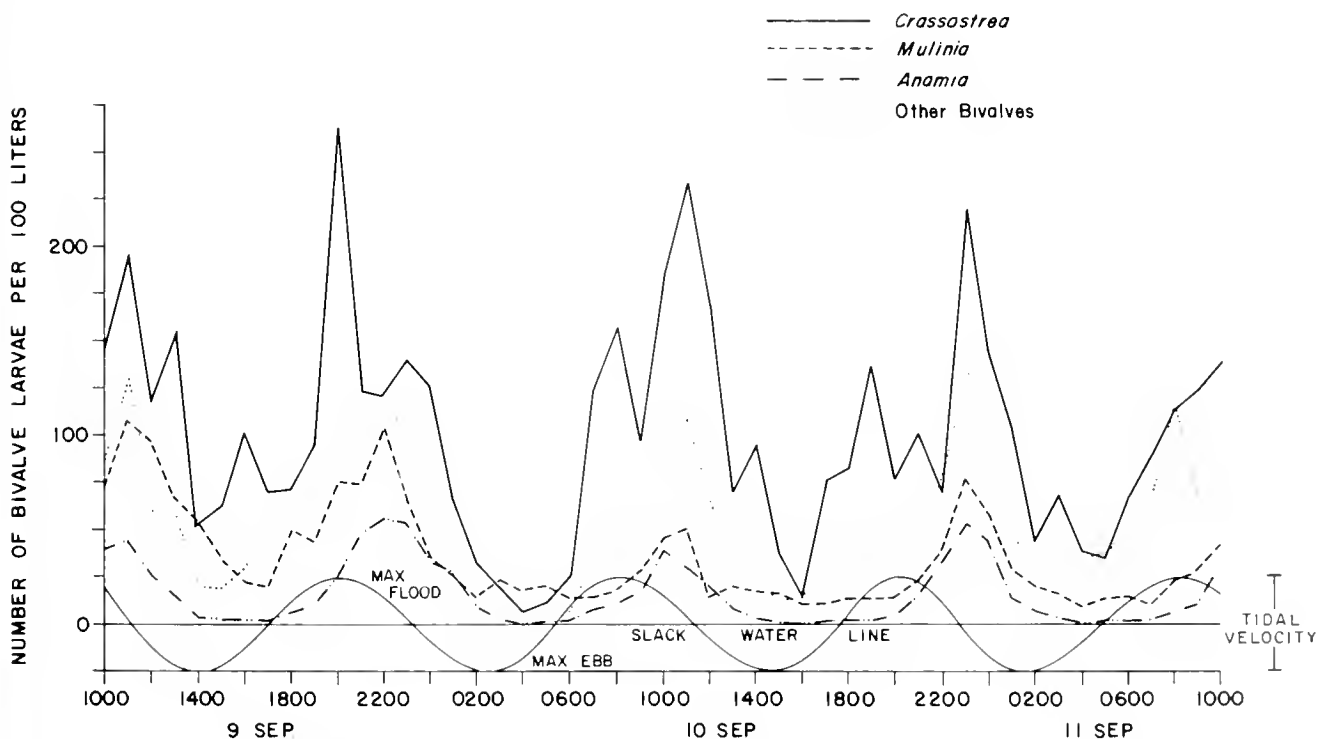

Figure 4. Cyclic abundance of bivalve larvae by species. Highest densities occurred between maximal flood and maximal ebb stages of tides.
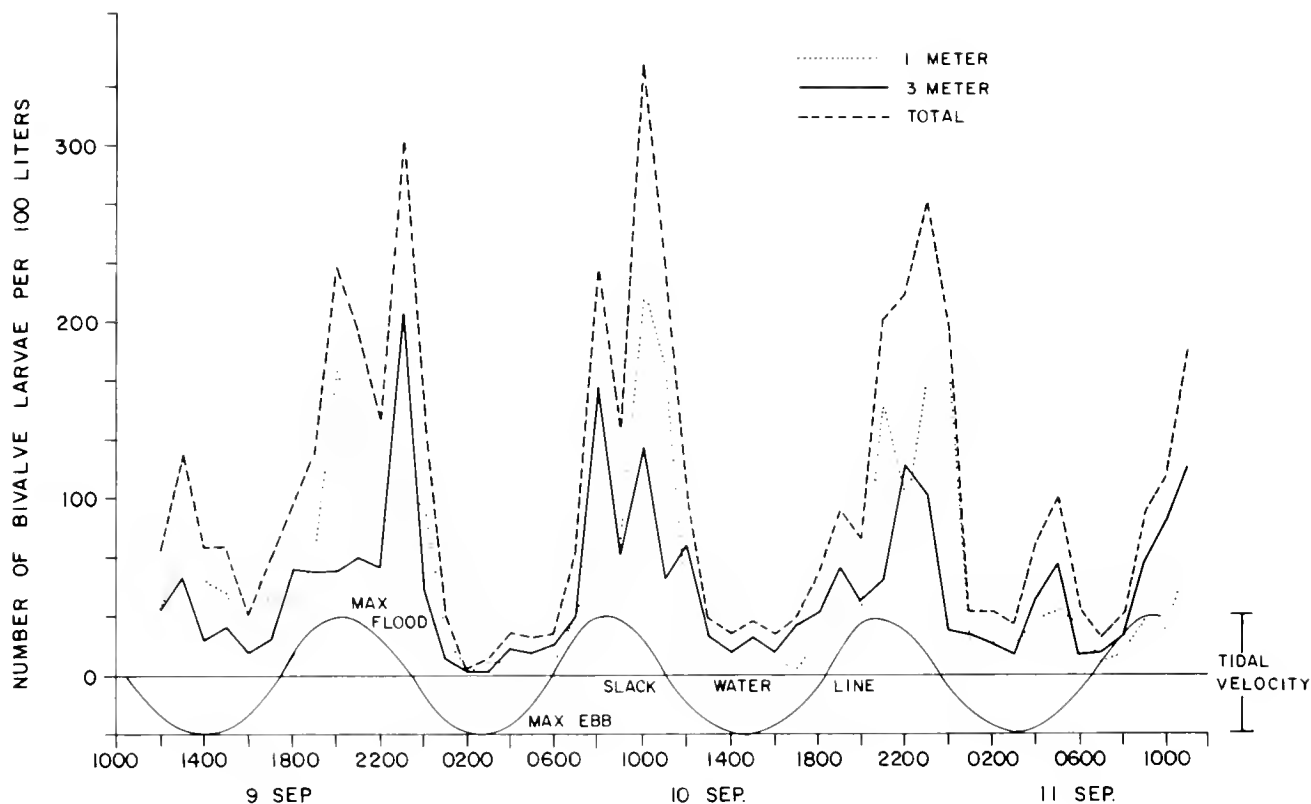
Figure 5. Density of bivalve larvae at surface and bottom over Brown Shoal oyster bed. Abundance of larvae was lower over shoals but cyclic patterns with tidal stages were similar for species and depths.

river ascent in the channel. Early-stage larvae appear to be recycled several times up the channel, out over the flats, and back down to Hampton Roads during their first days of pelagic life. Most larvae disappeared within less than 5 days; they were replaced by newly spawned larvae. Few larvae achieved advanced umbo stages during which they would have selected deeper layers of water thereby enabling them to ascend into the seed area.

My data and concept of transport and dispersal of bivalve larvae apply primarily to early-stage larvae (Figure 6). The seed area provides the larvae and Hampton Roads is a deep-mixing zone which facilitates advection of larvae upriver in the channel. These are primary but not exclusive roles for the two river sectors shown in the diagram. It is apparent from plankton sampling and spatfall patterns that new groups of young larvae are being introduced every week, or more frequently. Larvae in waters discharged into Chesapeake Bay are lost at an estimated flushing rate of 15% per tidal cycle (A. Kuo, Virginia Institute of Marine Science, Gloucester Point, VA; pers. comm.); this sums to 95% loss

of larvae in 10 days or 20 tidal cycles, the shortest probable duration of larval life in nature. Data on larval abundance near the river mouth are not available, but it is presumed from the spatfall gradients that eventually setting-size larvae are at least as abundant as at Brown Shoals. Hourly sampling during 5- and 3-day physical and biological studies in a 13-day period in September 1965 showed the scarcity of advanced oyster larvae in the James River. Larvae were not surviving in the James River long enough to grow to umbo larvae (3 to 5 days) and, therefore, could not utilize the net upriver channel flow in waters greater than 3 m depth. There are no data on losses of bivalve larvae by predation in nature, although my assumption is that the same predators present in the 1950's are still equally active in the 1960's and 1970's. Many pelagic larvae, including fish fry, coelenterates, ctenophores, as well as most adult bottom-living organisms with mucus and ciliary feeding mechanisms, capture bivalve larvae (Mileikovsky 1974, Andrews 1979). Most efficient as collectors are adult oysters on beds where mature larvae are most attracted by gregarious setting.

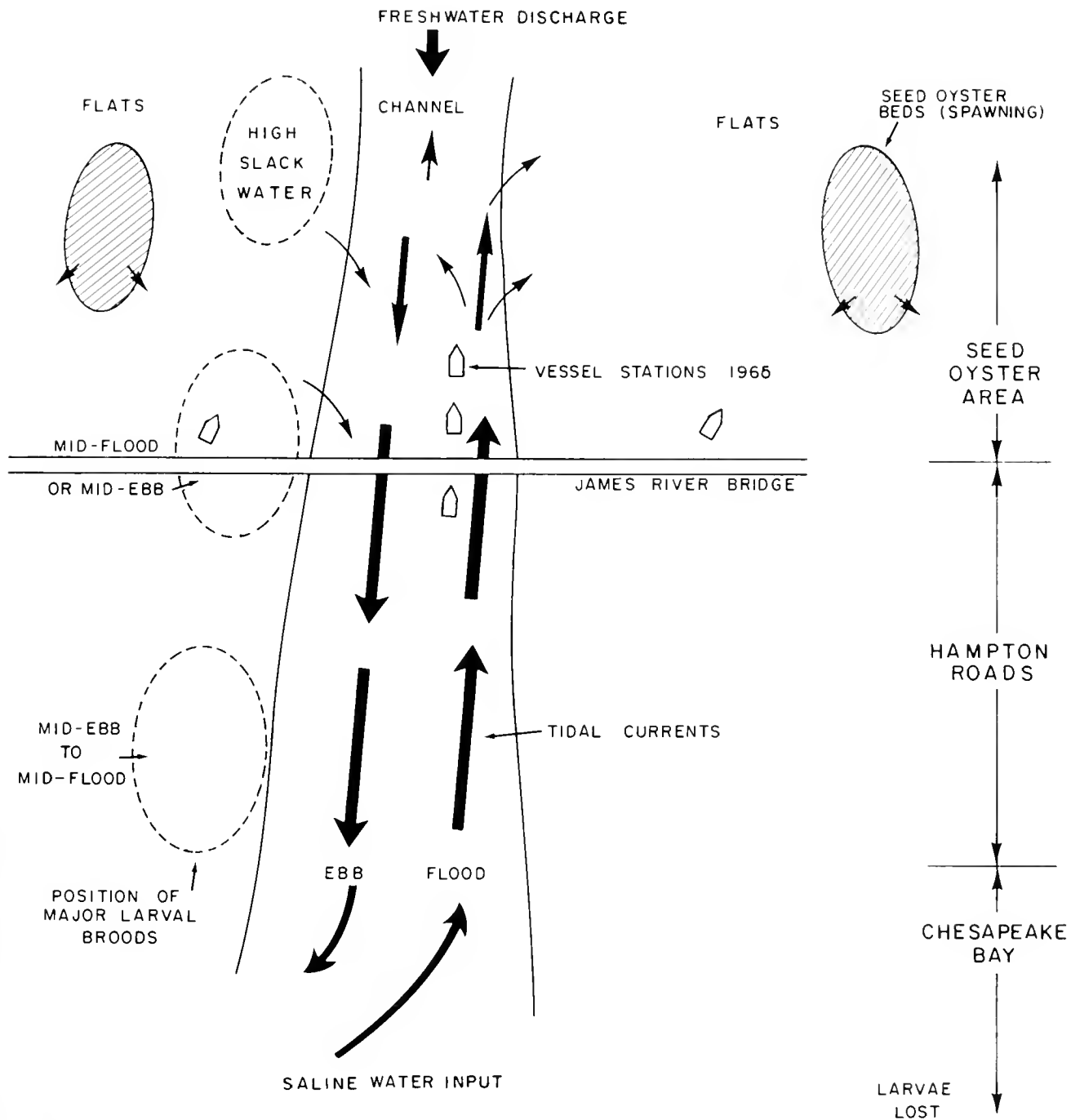TRANSPORT OF BIVALVE LARVAE IN THE JAMES RIVER

Figure 6. Diagram of a hypothesis of larval transport in James River. Oyster beds and larval broods are located only symbolically. Channel transport is emphasized, but transport of larvae occurs throughout cross sections of the river. Width of arrows suggests intensity of transport system and density of larvae. A tidal excursion is about 11 km in channel. The bridge and Deep Water Shoal are 19 and 46 km, respectively, above the river mouth.

Figure 6 emphasizes the importance of channel waters for transport of larvae upriver. Tidal excursions average about 11 km in the channel; this means that larvae located at the bridge could be carried to Wreck Shoal in one flood tide, or downriver to the middle of Hampton Roads in one ebb tide. In three years (1963–1965) of late-summer sampling in the Brown Shoal area, oyster larvae were rarely absent; this indicates that one or more broods were distributed at least 11 km above and below the bridge during a tidal cycle. The larval groups illustrated by ovals on Figure 6 are intended to suggest the location where larvae were most abundant at given tidal stages. The arrows suggest densities of larvae in the channel and at sites of dispersion over oyster beds. Most larvae carried upriver during flood tide appear to be carried back down the channel during ebb tide; a few must be trapped over shallow oyster beds or in meandering creeks by eddies and boundary effects (slowing of currents) of bottom and marginal features such as marshes. Apparently, advanced larvae at Wreck Shoal on 3 September 1964, which were abundant mostly in the channel, reached oyster beds in the seed area by slow advance in net upstream flow in deep channel currents.

Wood and Hargis (1971) reported on a 24-hour period of sampling (1 September 1965) during the same field study reported in this paper. Larvae showed the same patterns of abundance given in this report and also in the other days not reported by either of us. In their samples, oyster larvae were usually fewer than 100 per 300-ℓ sample, although early-umbo-stage larvae were relatively abundant. They reported physical data on circulation, salinity, temperature, and net flow based on seven complete tidal cycles of observation. These physical conditions apply equally well to plankton data presented in this paper for 9 to 11 September. The type C counter-clockwise circulatory pattern described by Pritchard (1955) prevails in the James River in late summer when freshwater discharge is low. Monthly river discharge averaged less than 28.3 m^3/s ($<$ 1,000 ft^3/s) for the months of August and September 1964 and 1965. Net upriver flows are greater on the northeastern side of the channel, and discharge is greatest downriver on the southwestern shore.

Wood and Hargis (1971) contended that oyster larvae on the bottom responded to salinity stimulation during flood tides, but they provided no data that showed selective swimming or distribution of larvae by depths. Vertical salinity gradients in Hampton Roads where larvae originate with each flood tide were less than 1 ppt from surface to bottom. If larvae rested on the bottom during ebb and low tides, they could respond to increasing salinities during flood tides (Haskin 1964), but evidence that larvae rest on the bottom is inconclusive. Carriker (1951) worked in high-salinity coastal bays where shallow water and strong pycnoclines prevented larvae from freely selecting strata for upriver transport. Both Carriker (1950) and Wood and Hargis (1971) support Nelson's hypothesis (Nelson and

Perkins 1931) that oyster larvae ascend estuaries by resting on the bottom during ebb tides and by swimming during flood tides. Data of Wood and Hargis (1971) comparing coal particles with larvae seem irrelevant to me because it has been clearly established that bivalve larvae can move vertically by their own powers of swimming. Larvae were found during all tidal stages whereas coal particles were observed only during strong currents. Larvae were most often abundant at high-slack water and there was no evidence that larvae descended during periods of slack currents. Larvae were least abundant in samples taken near the bottom during strong tidal currents when large numbers of fecal pellets (primarily from oysters) and sand grains were found in samples. This leads me to believe that larvae are actually trapped on the bottom during strong currents by the roiling effects of bottom drag and constant pelting–even though all are being carried by slow bottom currents. Dirty samples taken too close to the bottom always contained few larvae. If distribution of larvae were completely passive, they would spend both high- and low-slack periods on the bottom just as coal particles and fecal pellets do, but feeding time would be reduced. Losses of larvae to smothering and predation on the bottom may be as great as those from dispersal and predation during planktonic life.

Counts of larvae collected through 8 days (16 tidal cycles) show that the pattern of highest abundance from mid-flood to mid-ebb tides was regular and highly significant, but explanations of cyclic abundance vary in the literature. The important observations of the present study are: (1) total quantities of larvae at all stations before and after slack-high water were approximately equal; (2) persistence of early-stage larvae indicated that new broods were recruited frequently into the river; (3) older larvae were found most frequently in deeper waters and, therefore, in the channel; and (4) there was a noticeable decrease in density of larvae from the lower channel station to the upper one, only 4 km apart, at all tidal stages.

Larval broods are three dimensional. The term swarm is inappropriate for there is no evidence that larvae remain together or aggregate horizontally. Advanced larvae choose deeper strata in the water column effectively. Passive physical transport probably far outweighs in significance any results from selective motion by larvae, particularly during the first 5 days of planktonic life. Larvae do respond to pheromones when setting is about to occur. It is not known whether they can respond to food or other stimuli.

My scenario for the decline of setting in James River since 1960 assumes that loss of brood stocks to MSX disease in the lower river resulted in too few larvae to replenish oyster stocks in the seed area. It appears that broods of larvae are carried up and down the river several times with progressive thinning and dispersal of each brood. In the area sampled in 1965, near the James River Bridge, larvae probably moved up the channel and along the northeastern

shallow flats, then back down the channel and over the southwestern flats to Hampton Roads (Wood and Hargis 1971). Most larvae were lost by dispersion and predation in 3 to 5 days before they were stimulated to swim in deeper strata. New broods replaced old ones repeatedly. Spring tides and storms that increase tidal amplitude over the mean 0.72 m may cause some larvae to be trapped inshore and result in spatfalls. Because the same circulatory patterns still exist in James River, regular spatfalls every week for 3 months in the 1950's may be attributed to much larger populations of brood oysters and greater abundance of larvae in that period.

In the mid-1960's, Langley Wood (VIMS, Gloucester Point, Virginia, unpublished studies) constructed a vertical plexiglass cylinder about 2.5 m long and 0.3 m in diameter to study the swimming habits of oyster larvae. A strong light was mounted over the upper end and sampling ports were inserted at various levels. Larvae alternated between swimming upward in gyrals and falling slowly while resting for periods of a minute or so. When larvae bumped into one another they quickly retracted their velums. Pelagic larvae have two purposes: to distribute the species and to replenish adult stages (Galtsoff 1964). The velum provides a mechanism for swimming and feeding activities to meet these goals. Larvae must swim to eat. Resting for half of each tidal cycle on the bottom may require a doubling of the duration of larval life. In hatchery cultures, strong light causes swimming larvae to seek shade and curious distributional patterns visible to the naked eye are formed. In many estuaries, larvae are confronted with unfavorable natural conditions such as low temperatures or toxic compounds below surface waters (Quayle 1969). In these waters larvae are forced to swim continuously throughout their planktonic life regardless of dispersal effects.

I conclude that bivalve larvae swim continuously during larval life and that their dispersal and ultimate fates are strongly dependent on current regimes and flushing rates of estuaries. The bottom is a hazardous place for larvae to rest: a host of sedentary filter feeders become predators or imprison larvae in mucous-wrapped fecal pellets (Cerruti 1941, Mileikovsky 1974). Siltation is a serious threat on the bottom in channels where currents are strong. Prolonged duration of larval life and exposure to predators are major threats to survival in the James River with its relatively high flushing rates. The trap-type estuaries with their relatively intensive setting rates provide physical transport regimes that allow greater retention of larvae. If oyster larvae can persist in an estuary long enough to reach umbo size, a preference for deeper waters prevails and, in the case of the James River, they should be able to ascend the deep channel currents more effectively than in the poorly stratified trap-type estuaries. Observations from setting records indicate that the opposite occurs and that they are less successful in remaining in strong flushing-type estuaries. This implies that passive physical transport predominates over larval reactions to physical and chemical stimuli to select favorable current strata. Presumably, more intensive oyster setting in Delaware Bay can be attributed to the large size of the estuary with lower freshwater-discharge rates and to its wide shallow flats; only the upper seed area sector exhibits type-C circulation in summer, and flushing rates in the widened lower sector (Hidu and Haskin 1971) are probably much lower than in James River.

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BIOLOGICAL CONTROL OF FOULING ALGAE
IN OYSTER AQUACULTURE

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ABSTRACT The periwinkle *(Littorina littorea* Linné) provided excellent biological control of *Ectocarpus* sp., *Enteromorpha* sp., *Ulva* sp., and pennate diatoms, all of which foul oyster-rearing boxes. The addition of periwinkles ($200/m^2$) to 1-mm mesh-covered rearing boxes containing juveniles of the European flat oyster *Ostrea edulis* Linnaes promoted a significantly higher oyster growth rate (t-test; $p = 0.05$). Examination of the means obtained from a 5-week study showed a 30% increase in oyster growth rate when periwinkles were added, in comparison to the unmanipulated control. There was no significant difference (t-test; $p = 0.05$) in oyster growth rates when the culture boxes were either brushed once a week or periwinkles were added. A density range of 0 to 1,600 periwinkles/m^2 of oyster-rearing surface was examined in culture boxes covered with 6-mm mesh. Similar oyster growth rates were obtained with densities between 300 and 1,600 periwinkles/m^2 of oyster-rearing surface. Isopods (*Idotea balthica* Pallas) at a density of $125/m^2$ of oyster-rearing surface were not effective as a biological control agent.

KEY WORDS: biological control, oysters, periwinkles, algal fouling, *Ostrea edulis, Littorina littorea*, oyster culture

INTRODUCTION

Oyster-rearing boxes, trays, and lantern nets quickly foul with algae, mussels, bryozoans, sponges, and other marine organisms which restrict the flow of water and, consequently, the availability of phytoplankton to the oysters. Michael and Chew (1976) examined the effect of progressive fouling in off-bottom oyster culture in the state of Washington and correlated it with a decline in the growth rate of the Pacific oyster *Crassostrea gigas* Thunberg.

The traditional methods of coping with fouling in oyster culture include routine manual scraping and brushing, air-drying, controlled burning, pesticides, and high-pressure spraying to remove fouling organisms (Arakawa 1980). Clime and Hamill (1979) found that high-pressure spraying with a portable 378.5 to 567.7-ℓ/min (100 to 500-gal/min) capacity pump reduced marine fouling on oyster-culture gear in Maine. The cleaning schedules included bi-weekly treatments for small mesh enclosures and monthly cleaning for lantern nets and larger mesh enclosures during the height of the growing season. MacLeod (1974) investigated the use of a hot-water dip treatment for control of fouling organisms on oyster-culture gear. Huguenin and Huguenin (1982) examined the use of expanded metal mesh of a copper-nickel alloy in shellfish trays. Although these procedures are effective, they are both expensive and time consuming. Dr. E. Scura (Aquatic Farms, Hawaii, pers. comm.) estimated that 20% of the market price of intensively cultured oysters reflected the costs associated with reducing fouling organisms during the rearing stages. In Nova Scotia during 1983, the members of the Ostrea Edulis Cooperative Association Ltd. allocated more than half of the labor time associated with rearing oysters to cleaning of fouling from oysters and culture gear. Thus, fouling has traditionally been a costly problem in terms of equipment and labor costs as well as reduced oyster growth rates. An efficient, inexpensive means of ensuring maximum water flow about the oysters is greatly needed.

Biological control is the utilization of natural or exotic species to control the density of undesirable organisms. Hidu et al. (1981) inadvertently enclosed a rock crab *Cancer irroratus* Say in a tray of over-wintering yearling European oysters and found that the typical thick mat of fouling organisms did not develop. By selecting crabs of a distinct size range, Hidu et al. (1981) demonstrated that the introduction of crabs to oyster culture may provide a means of biologically controlling the growth of fouling organisms. Movement by the crab was also believed to reduce silt accumulation on the oysters. While suitable for the culture of large oysters, crabs prey upon small oysters and can only be used with great care as a biological control agent with juvenile oysters. The fouling problem is more acute with juvenile oysters because they can not withstand the damage incurred by traditional cleaning methods. Also, the small-mesh screen needed to retain juvenile oysters fouls more quickly and accentuates the fouling problem. Because snails and isopods have demonstrated the ability to consume algae (Shacklock and Croft 1981, Steneck and Watling 1982), we investigated the usefulness of periwinkles and isopods as biological control agents in juvenile oyster culture. Bequaert (1943) noted that the herbivorous habits of *L. littorea* were sometimes used to keep oysters free of algal growth. We felt that such an application might be useful in oyster aquaculture.

MATERIALS AND METHODS

Juveniles of the European oyster *Ostrea edulis* Linnaes were studied in Sambro Harbour, Nova Scotia (44°28′51″N, 63°34′21″W). The water temperature range was 12 to 17°C and the salinity range was 29 to 31 ppt during the experimental period. The oysters were reared in boxes with wooden sides which were covered on the top and bottom with plastic screening. Two sets of three vertically suspended culture boxes were hung from a floating boom near each other. The top box in each set was approximately 20 cm beneath the water surface with subsequent boxes approximately 25 cm apart. Oyster growth rate was assessed using change in volume or weight over the experimental period. An empty box with plastic screen was suspended between the experimental box sets. A small piece of mesh was clipped bi-weekly from this box for a microscopic examination of the colonizing organisms throughout the experimental period. The fouling organisms were identified and the abundance of each was expressed as a percentage of the total fresh weight biomass of all fouling organisms.

The first experiment was conducted from 7 July to 12 August 1981. The culture boxes were 83 X 60 X 6 cm and were covered with 1-mm plastic screening. Each of the six boxes was divided by wooden slats into four equal compartments, with each box receiving one of the following four treatments: the addition of 24 periwinkles *(Littorina littorea)* $(200/m^2)$ approximately 2 cm in diameter; the addition of 13 isopods *(Idotea balthica)* $(125/m^2)$ approximately 3 cm in length; weekly manual brushing of the screen mesh; and an unbrushed control. Juvenile oysters, approximately 5 mm in diameter, were stocked in the boxes at an initial "density" of 600 g/m^2.

The second experiment was conducted from 5 July to 3 October 1982. A similarly arranged culture unit was used with boxes measuring 30 X 30 X 6 cm and covered with 6-mm mesh plastic screen. The six boxes were divided into four equal compartments and suspended in two units, each with three boxes. The following series of treatments was replicated at each of the three-box positions (upper, middle and lower): weekly manual brushing of the mesh; 0 (contol), 2, 5, 10, 15, 20 and 25 periwinkles in each compartment which corresponds to 0.01, 0.03, 0.05, 0.08, 0.10 and 01.3 periwinkles/m^2. The oysters used were approximately 2 cm in diameter and the oyster stocking "density" was 8,000 g/m^2.

RESULTS AND DISCUSSION

Littorina littorea proved to be an excellent biological control agent for reducing algal fouling on the oysters and on the screens covering the oyster-rearing boxes. The addition of 200/m^2 periwinkles to 1-mm mesh-covered rearing boxes containing juvenile European oysters was shown to yield a significantly higher (t-test; p = 0.05) oyster growth rate (Table 1). Examination of the means obtained from a 5-week study showed an approximate 30% increase in oyster growth rate (Set 1, 36%; Set II, 25%) when periwinkles were added compared with the unbrushed control (Table 1). The major fouling organisms were *Ectocarpus* sp. (90%), *Enteromorpha* sp. (3%), *Ulva* sp. (1%), and pennate diatoms (5%). Animal fouling accounted for less than 1% of the total fouling biomass. There was no apparent change in the species composition of the fouling organisms throughout the experimental periods. On the basis of visual inspections, the periwinkles kept the mesh cleaner than that obtained with a weekly manual scrubbing. There was no significant difference (t-test; p = 0.05) in oyster growth rates when the culture boxes were brushed once a week or periwinkles were added. *Idotea balthica* did not actively graze the fouling organisms which collected on the plastic screen, and the growth rate of the oysters

TABLE 1.

Increase in volume (mℓ) and the calculated growth rate (% volume increase day^{-1}) of *Ostrea edulis* cultured in boxes with unbrushed screens, with brushed screens, with periwinkles, and with isopods. The initial size of the oyster was approximately 5 mm in diameter and the experimental period was 5 weeks (7 July to 12 August 1981).

Box Position	Unbrushed		Brushed		With Periwinkles		With Isopods	
	Δ Volume	% day^{-1}	Δ Volume	% day^{-1}	Δ Volume	% day^{-1}	Δ Volume	% day^{-1}
Set 1								
Upper	190	4.1	240	4.8	240	4.8	170	3.7
Middle	170	3.7	190	4.1	210	4.4	210	4.4
Lower	120	2.7	200	4.2	200	4.2	120	2.7
$\bar{X}$	160	3.5	210	4.4	217	4.5	167	3.6
SD	36	0.7	26	0.4	21	0.3	45	0.8
Set II								
Upper	260	5.0	280	5.2	310	5.5	260	5.0
Middle	220	4.5	320	5.6	300	5.4	200	4.2
Lower	180	3.9	190	4.7	220	5.2	140	3.8
$\bar{X}$	220	4.5	263	5.2	277	5.4	200	4.3
SD	40	0.6	67	0.5	49	0.2	60	0.6

reared in such compartments did not differ significantly (t-test; p = 0.05) from that of the oysters in the unbrushed (control) compartments. Using a comparable isopod density, Shacklock and Doyle (1983) found that *I. balthica* voraciously grazed *Ectocarpus* sp., a brown seaweed which grows epiphytically on *Chondrus crispus* in tank cultures. Perhaps in the present experiment a higher isopod density would have negated the fouling rate in the oyster-rearing boxes. Oyster boxes suspended in the water column may not provide an adequate habitat for isopods; perhaps their feeding behavior is altered in that setting. From the data in Table 1, it is clear that higher oyster growth rates were obtained in box Set I compared to box Set II. The difference may have been the result of their relative position in the bay as box Set II was downstream from box Set I with respect to the food source. All other parameters were the same in each box set.

An examination of a periwinkle density range from 0 to 1,600/m^2 of mesh-rearing surface, when a 6-mm mesh size was used, indicated little change in oyster growth rates between 300 and 1,600 periwinkles/m^2 of screen (Figure 1). The optimal periwinkle density would be expected to vary as a function of the degree of fouling and with factors that influence the periwinkle grazing rate (e.g., temperature).

There are many advantages to utilizing periwinkles for biological control of fouling organisms in juvenile oyster culture. Periwinkles are herbivors; therefore, they do not prey on oysters as do crabs and other organisms. *Littorina littorea* is extremely abundant in western Europe and in northeastern North America and locally exceed densities of 150 periwinkles/m^2 in the low intertidal zone. The periwinkle can completely withdraw its soft tissue into its shell, thus protecting itself against desiccation when the oyster boxes are removed from the water for data collection or transportation. There was no evidence of erosion of the mesh fibers as a result of the periwinkles grazing along the plastic screens. The major advantage of using a biological control agent such as a periwinkle is the reduction in costs associated with cleaning algal fouling organisms. As water flow and phytoplankton availability are greatly
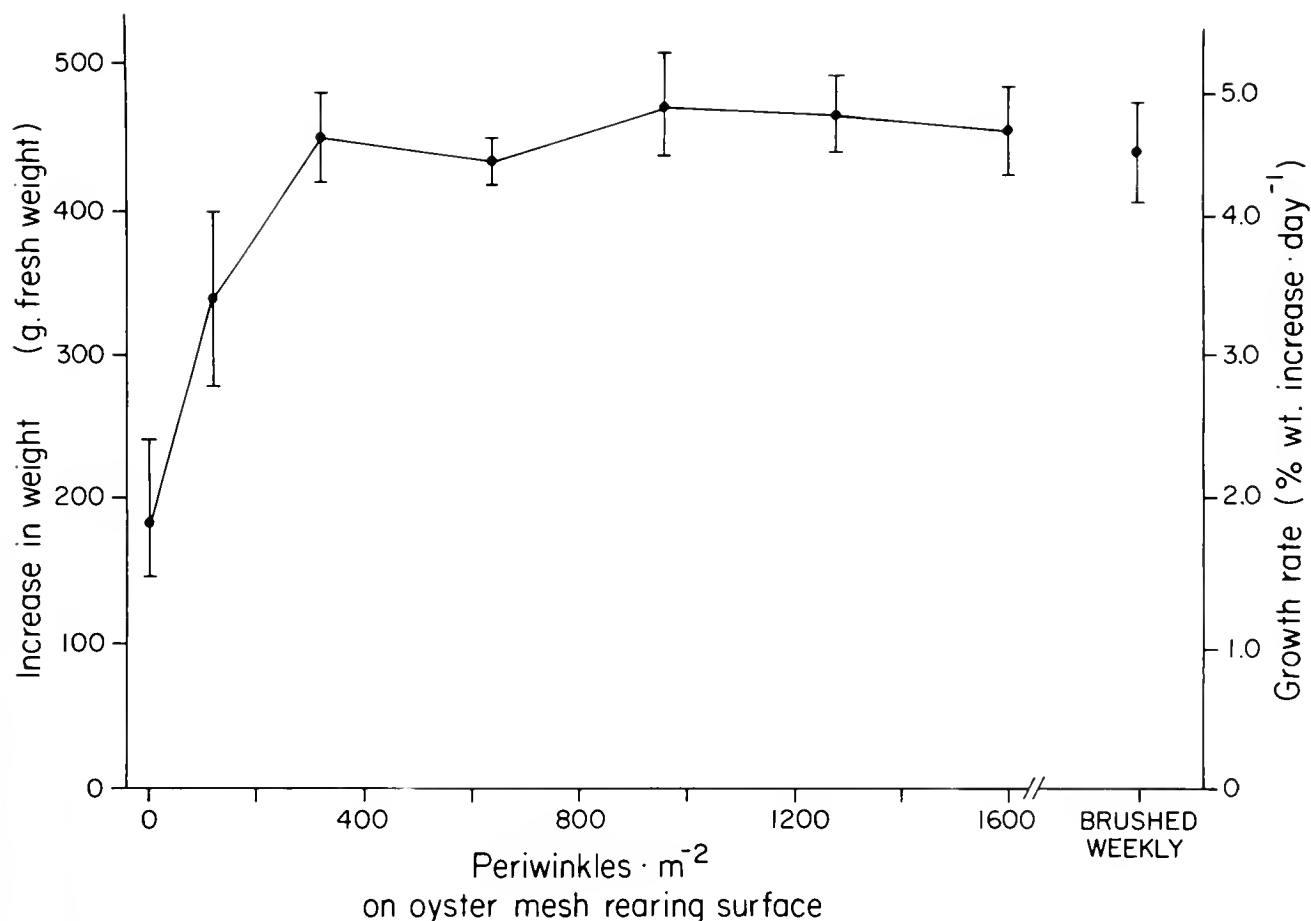

Figure 1. Increase in weight (g fresh weight) and the corresponding calculated growth rate (% weight increase day^{-1}) of *Ostrea edulis* cultured with *Littorina littorea* at various densities and compared with a weekly, manual mesh-brushing treatment. The initial size of the oysters was approximately 2 cm in diameter and the mesh used on the rearing boxes was 6 mm. The experimental duration was 12 weeks (5 July to 3 October 1982). Standard deviations are shown (n = 3).

enhanced for juvenile oysters cultured with periwinkles, the need to transfer oysters on to larger mesh sizes, as is presently the practice (Clime and Hamill 1979), is reduced. Such cost reductions will greatly improve the profitability of off-bottom oyster culture.

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A STUDY OF GLUCOSE, LOWRY-POSITIVE SUBSTANCES, AND TRIACYLGLYCEROL LEVELS IN THE HEMOLYMPH OF *CRASSOSTREA VIRGINICA* (GMELIN)

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ABSTRACT   Oysters, *Crassostrea virginica* (Gmelin), were maintained in the laboratory under controlled conditions of temperature and salinity. Levels of several hemolymph constituents were analyzed. Average values of hemolymph glucose, Lowry-positive substances, and triacylglycerols were 8.83 ± 1.98 mg/100 mℓ ($\pm$ SE), 11.0 ± 1.89 mg/mℓ ($\pm$ SE), and 43.2 μg/100 mℓ, respectively. Hemolymph glucose values varied over a wide range. No deleterious effects of this variance (as judged by mortality rates) could be detected. Groups of animals with initial hemolymph glucose levels of 23.1 to 25.0 mg/100 mℓ survived as long as those with initial values of 5.3 to 8.4 mg/100 mℓ. Oysters held at constant water temperatures and salinities tended to maintain the concentration of their hemolymph glucose and Lowry-positive substances over a 27-day period of starvation; hence, some type of regulatory mechanism is involved in controlling the levels of these metabolites in oyster hemolymph. Extremes in environmental conditions appear to affect the concentrations of these metabolites in hemolymph. Groups of oysters maintained in sea water at a temperature of 4°C had significantly higher ($p \leq 0.05$) levels of hemolymph glucose and Lowry-positive substances than groups held at 20°C. Groups of oysters maintained at a low ambient salinity (12 ppt) had significantly lower ($p \leq 0.05$) levels of hemolymph glucose and Lowry-positive substances than groups kept in water of 18 ppt and 24 ppt salinity.

KEY WORDS: oyster, *Crassostrea virginica*, hemolymph, glucose, regulation

INTRODUCTION

Traditionally, the physiological and nutritional conditions of oysters have been monitored by evaluating tissue glycogen content (Gabbott and Walker 1971, Willis et al. 1976). The deposition and utilization of not only glycogen but also lipid by the American oyster may be influenced by a number of factors. Seasonal variations in tissue glycogen and lipid content, which are keyed to the reproductive cycle, are well documented (Galtsoff 1964, Krishnamoorthy et al. 1979, Swift et al. 1980). The effects of starvation on these metabolic reserves in oysters have been examined (Riley 1976, Willis et al. 1976, Swift et al. 1980), as have environmental conditions which may also affect the rate of synthesis or utilization and, therefore, content of metabolic reserves.

Several groups have investigated either the whole animal response or the response of selected excised tissues to changes in temperature and salinity. Ruddy et al. (1975) examined the growth rate of *Crassostrea virginica* (Gmelin) during exposure to a warm water temperature (14 to 19°C). Levels of each of the major classes of metabolites (carbohydrate, protein, and lipid) increased in these animals. At the same time gonadal development occurred four months earlier than usual. Similar increases in biochemical reserves have been observed in *Crassostrea gigas* (Thurnberg) and *Ostrea edulis* (Linné) (Mann 1979). Percy and Aldrich (1971), Percy et al. (1971), and Bass (1977) monitored the effect of changes in ambient water temperature and salinity on oxygen consumption of excised gills, mantle, and adductor muscle of *C. virginica*. These reports agree that, with increasing temperature or decreasing salinity, oxygen use increases. When subjected to extremes of temperature and salinity, these animals used more oxygen (Shumway and Koehn 1981). These data imply that the metabolic rate has increased and, thus, utilization of metabolic reserves has increased, resulting in a decrease in tissue content of glycogen and lipid.

Despite the proven usefulness of data on tissue composition, the processes required to obtain them are cumbersome and time consuming. In contrast, more complete information concerning the nutritional and physiological conditions of mammalian organisms may be obtained easily and rapidly by analysis of blood metabolites. Unfortunately little is known regarding the metabolite levels in the hemolymph of *C. virginica*. Hand and Stickle (1977) studied the effect of tidal-like fluctuations in salinity of ambient sea water on pericardial fluid composition of the oyster. Ion concentrations, except K^+, were found to be isoionic to the various ambient salinity regimes; ninhydrin-positive substances ranged from 1.5 to 6.0 mM.

The lack of suitable data in the literature for establishing baseline values for hemolymph glucose, protein, and triacylglycerol levels in *C. virginica* prompted the following studies. Glucose, total Lowry-positive substances (LPS), and triacylglycerols were examined in hemolymph from groups of oysters subjected to: (1) starvation, (2) different ambient temperatures, and (3) different ambient salinities.

MATERIALS AND METHODS

Oysters (*C. virginica*), purchased commercially (Capt. White and Sons, Seafood, 110 Main Avenue, SW, Washington, DC 20024), had been harvested two or three days before arrival in the laboratory. The height of the animals, measured as the distance from the hinge to the extreme ventral margin of the shell, ranged from 7 to 12 cm. Before any data were gathered the oysters were cleansed in tap water with the aid of a wire brush and acclimated to laboratory conditions for three days. Up to 20 unfed individuals were held in an aquarium in approximately 7 ℓ of artificial sea water (Instant Ocean, Aquarium Systems Inc., 33208 Lakeland Blvd., Eastlake, OH 44094). The glass holding tanks were arranged so that the sea water was drawn off at the bottom of each tank, and then pushed up through a water-cooled condenser to the top of the holding tank by compressed air (Swift et al. 1975). A refrigerated bath and circulator was used to control the water temperature. Sea water in the tank was changed every two days and the tank thoroughly rinsed at those times.

Hemolymph was collected with a small syringe from the pericardial cavity of carefully opened oysters. The hemolymph was placed in an ice-cooled centrifuge tube. Cellular debris were separated from the hemolymph by centrifugation at $1,000 \times g$ for 20 minutes at $4°C$. The supernatant liquid was transferred to a small vial and stored at $-10°C$ before glucose, total Lowry-positive substances (LPS), and triacylglycerol determinations were accomplished. Glucose was analyzed using the glucose oxidase method (Bergmeyer and Bernt 1974), total Lowry-positive substances were estimated according to Lowry (Lowry et al. 1951), and triacylglycerol was analyzed by the acetylacetone test (Fletcher 1968) with a slight modification. Hemolymph that was pooled from 3 to 4 oysters was extracted with *n*-heptane; 1 mℓ of the upper layer was removed for analysis. After the aliquot was dried completely under a stream of air, 2.0 mℓ of isopropanol were added. Thereafter the procedure was the same as described by Fletcher (1968).

Hemolymph lipids were extracted by the Folch procedure (Folch et al. 1957). The chloroform layer, remaining after the aqueous NaCl wash, was evaporated to dryness under reduced pressure. The lipids were redissolved in a minimal quantity of 2:1 (v/v) chloroform:methanol and separated by thin-layer chromatography on silicic acid using *n*-hexane:diethyl ether:glacial acetic acid at a volumetric ratio of 70:30:1 (Malins and Mangold 1960). The spots were visualized by iodine vapor retention or by ultraviolet fluorescence after spraying the chromatogram with 0.2% 2′:7′-dichlorofluorescein in 95% ethanol.

To examine the effect of selected environmental conditions on the levels of metabolites in oyster hemolymph, groups of unfed animals were held in tanks for up to 27 days under the following conditions: (1) in 24 ppt sea water at temperatures of 4, 10, 15, or 20°C, and (2) in 12,

18, or 24 ppt sea water at 20°C or 15°C. Data were analyzed for significance ($p \leqslant 0.05$) by the Student's *t*-test.

RESULTS

Oysters obtained throughout the course of this study did not have significantly different initial levels of hemolymph glucose (Table 1). Overall hemolymph glucose concentrations averaged 8.83 ± 1.98 mg/100 mℓ ($\pm$ SE) and ranged from 1.9 to 25.0 mg/100 mℓ. Hemolymph LPS levels averaged 11.0 ± 1.89 mg/mℓ and ranged from 3.17 to 29.5 mg/mℓ. Hemolymph triacylglycerol values were quite low averaging 43.2 μg/100 mℓ and ranged from 3.3 to 200 μg/100 mℓ.

TABLE 1.

Initial hemolymph glucose, Lowry-positive substances (LPS) and triacylglycerol levels in groups of oysters.

Month	N	Glucose (mg/100 mℓ)*	LPS (mg/mℓ)*	Triacylglycerol (μg/100 mℓ)**
December	11	15.80 ± 6.54	26.00 ± 4.18	11.7
January	6	9.18 ± 2.18	18.60 ± 3.18	25.0
February	12	8.96 ± 1.46	19.40 ± 4.18	15.6
March	20	12.90 ± 2.28	14.10 ± 1.30	--
April	108	8.41 ± 2.50	12.10 ± 2.34	26.3
May	6	3.14 ± 1.22	8.08 ± 1.41	30.0
June	36	9.09 ± 2.11	8.02 ± 2.37	43.9†

*Mean values $\pm$ SE

**Mean values obtained by pooling hemoymph from 3 or more individuals

†76.7 μg/100 mℓ if values of 150 and 200 μg/100 mℓ are included

No free or nonesterified fatty acids could be detected in oyster hemolymph using standard analytical techniques or after lipid extraction followed by thin-layer chromatography. This is in agreement with results of other lipid analyses of oyster tissues (Watanabe and Ackman 1977, Bunde and Fried 1978, Ghassemieh 1978).

Oysters held at constant temperature and in sea water of constant salinity tended to maintain their hemolymph glucose, LPS, and triacylglycerol concentrations over a 27-day period of starvation (Tables 2, 3, and 4); however, extremes in external conditions appear to affect the concentrations of these metabolites. Groups of unfed oysters maintained in 24 ppt artificial sea water at temperatures of 4°C had significantly higher ($p \leqslant 0.05$) levels of hemolymph glucose and LPS when compared to values obtained from oysters kept at 20°C. Oysters held at 4°C had hemolymph glucose values of 19.3 ± 3.5 mg/100 mℓ while those kept at 20°C had hemolymph glucose values of 8.41 ± 1.4 mg/100 mℓ. Similarly the mean LPS values were 17.56 ± 1.42 mg/mℓ and 9.76 ± 0.85 mg/mℓ for the animals at 4°C and 20°C, respectively. At a low ambient salinity of 12 ppt, oyster hemolymph glucose and LPS concentrations were significantly ($p \leqslant 0.05$) decreased when compared to the values found in oysters kept in water of 18 and 24 ppt (Tables 5 and 6).

TABLE 2.

Hemolymph glucose levels* (mg/100 mℓ) in starved oysters maintained in 24 ppt sea water at different temperatures.

	Temperature (°C)			
Number of Days	4	10	15	20
3	23.4 ± 11.2	9.18 ± 2.17	7.72 ± 1.83	5.33 ± 1.19
7	23.1 ± 10.6	10.7 ± 2.04(5)	6.63 ± 1.75	8.38 ± 2.14
14	13.2 ± 2.59[a]	11.3 ± 1.74	11.7 ± 3.81	6.43 ± 1.25[b]
24	19.6 ± 4.07(5)	— —	10.2 ± 2.81	13.3 ± 6.02(5)
27	13.3 ± 10.0(3)[a]	— —	— —	5.92 ± 0.904[b]
Group Mean	19.3 ± 3.52[a]	10.3 ± 1.11[b]	9.06 ± 1.33[b]	8.44 ± 1.43[b]

*Mean value obtained from six individuals ± SE, unless otherwise indicated. Number in parenthesis shows number of oysters used. Means assigned the same or no superscript were not significantly different. Means assigned different superscripts were different at p ≤ 0.05 level (compared across groups).

TABLE 3.

Hemolymph Lowry-positive substance levels* (mg/mℓ) in starved oysters maintained in 24 ppt sea water at different temperatures.

	Temperature (°C)			
Number of Days	4	10	15	20
3	26.0 ± 4.18[a]	18.6 ± 3.18	19.4 ± 4.18 (5)	10.1 ± 2.23(3)[b]
7	15.1 ± 1.52	14.5 ± 2.86	16.8 ± 1.32(5)	12.1 ± 2.02(5)
14	14.1 ± 1.17	15.1 ± 1.68	21.0 ± 4.59	6.7 ± 1.23
24	17.1 ± 1.17(5)[a]	— —	17.7 ± 4.59	11.1 ± 1.84(5)[b]
27	12.3 ± 1.64(3)	— —	— —	8.71 ± 1.93
Group Mean	17.5 ± 1.42[a]	16.1 ± 2.57	18.7 ± 3.56	9.76 ± 0.85[b]

*Mean value obtained from six individuals ± SE, unless otherwise indicated. Numbers in parenthesis show number of oysters used. Means assigned the same or no superscript were not significantly different. Means assigned different superscripts were different at p ≤ 0.05 level (compared across groups).

TABLE 4.

Hemolymph triacylglycerol levels* (μg/100 mℓ) in starved oysters maintained in 24 ppt sea water at different temperatures.

	Temperature (°C)			
Number of Days	4	10	15	20
3	11.7	25.0	6.25	16.9
7	13.4	23.8	6.25	55.0
14	8.33	6.25	6.25	47.5
24	6.25	— —	25.0	113.0
27	— —	— —	— —	27.3

*Pooled samples from 3 to 6 oysters.

DISCUSSION

Hemolymph glucose levels have been examined in other fasting molluscan species. In the terrestrial snail, *Stropho-cheilus oblongus* (Müller), hemolymph glucose values ranged from 2.5 mg/100 mℓ to 16.88 mg/100 mℓ (Marques and Falkmer 1976). Hemolymph glucose levels in the freshwater pulmonate snail, *Lymnaea stagnalis jugularis* (Say), ranged from 1.86 to 5.68 mg/100 mℓ ($\bar{X}$ = 3.0) and 1.9 to 4.0 mg/100 mℓ ($\bar{X}$ = 2.9) in separate investigations (Friedl 1968, 1971). Hemolymph glucose concentrations in two freshwater bivalve molluscs, *Anodonta cygnea* (Linné) and *Unio pictorum* (Linné) averaged 9.4 ± 0.49 mg/100 mℓ and 14.0 ± 1.6 mg/100 mℓ, respectively (Plisetskaya et al. 1978). The hemolymph glucose level in the Atlantic deep sea scallop, *Placopecten magellanicus* (Gmelin), was 2.6 ± 0.6 mg/100 mℓ (Thompson 1977); and the hemolymph glucose concentration in another marine bivalve, *Mytilus edulis* Linné, lies between 16.0 and 37.0 mg/100 mℓ (Bayne 1973).

Inspection of these data leads to the conclusion that hemolymph glucose values during fasts in several molluscan species may vary over a wide range and are not directly related to terrestrial, freshwater or marine habitats. Thus, it may be inferred that these animals, including the oyster *C. virginica*, are more tolerant of larger variations of glucose concentrations in circulatory fluids than mammals. In this study, no deleterious effects of variations in hemolymph glucose levels could be detected. Groups of oysters with initial hemolymph glucose levels of 23.0 to 25.0 mg/100 mℓ survived as long as those with initial hemolymph glucose values of 5.3 to 8.5 mg/100 mℓ.

TABLE 5.

The effect of ambient water salinity on hemolymph glucose levels* (mg/100 m ℓ) of starved oysters.

	Temperature (°C)				
	20			15	
	Salinity (ppt)				
Number of Days	12	18	24	18	24
3	3.14 ± 1.22(5)	7.08 ± 2.58(5)	5.33 ± 1.19	10.2 ± 1.09(5)	7.87 ± 1.82
7	2.46 ± 0.47(5)	3.74 ± 0.92(5)	8.38 ± 2.14	7.26 ± 0.88(5)	6.63 ± 1.76
14	3.98 ± 0.69	2.88 ± 0.75(5)	6.43 ± 1.25	2.16 ± 0.51(5)	11.7 ± 3.82
24	--	3.72 ± 0.93(5)	13.3 ± 6.02(5)	4.58 ± 0.97(5)	10.2 ± 2.86
27	--	--	5.92 ± 0.90	--	--
Group Mean	3.24 ± 0.59	4.57 ± 1.00	6.72 ± 0.92[b]	6.53 ± 1.00[b]	9.02 ± 1.58[b]

*Mean values obtained from six individuals ± SE. Number in parenthesis shows number of oysters used. Means assigned the same or no superscript were not significantly different. Means assigned different superscripts were different at p ≤ 0.05 level (compared across groups).

TABLE 6.

The effect of ambient water salinity on hemolymph Lowry-positive substance levels* (mg/m ℓ) of starved oysters.

	Temperature (°C)				
	20			15	
	Salinity (ppt)				
Number of Days	12	18	24	18	24
3	8.08 ± 1.41	12.2 ± 2.41(3)	10.1 ± 2.23(5)	--	19.4 ± 4.18(5)
7	5.98 ± 1.70(4)[a]	6.51 ± 0.73(4)[a]	12.1 ± 1.23(5)[b]	3.17 ± 0.71(5)[a]	16.8 ± 1.32[b]
14	8.68 ± 0.96(4)[a]	9.99 ± 1.99(4)	6.73 ± 1.23	9.48 ± 1.74	18.3 ± 4.61
24	--	--	11.1 ± 1.84(5)	7.68 ± 1.94(5)	17.7 ± 4.15
27	--	--	--	--	--
Group Mean	6.07 ± 0.91[a]	9.31 ± 1.15[b]	9.64 ± 1.17[b]	6.78 ± 1.15[b]	17.5 ± 2.10[b]

*Mean values obtained from six individuals ± SE. Number in parenthesis shows number of oysters used. Means assigned the same or no superscript were not significantly different. Means assigned different superscripts were different at p ≤ 0.05 level (compared across groups).

During the course of these studies hemolymph glucose levels were relatively stable within test groups. This indicates that some type of regulatory mechanism functions in the oyster. There is no direct evidence for the regulation of hemolymph glucose in other molluscs; however, indirect evidence concerning various aspects of this physiological mechanism has been published. Enzymatic activities which are necessary for the postulated regulation have been identified in several molluscs. For example, hexokinase and glycogen phosphorylase activities have been reported in *Pecten maximus* (Linné), *O. edulis, Ensis ensis* (Linné), *Chlamys varius* (Linné) (Zammit and Newsholme 1976), and *C. gigas* (Nakamuro et al. 1980). Glycogen synthase activity has been studied in *M. edulis* (Cook and Gabbott 1978, Gabbott et al. 1979).

Of the hormones known to affect mammalian blood glucose levels, only insulin has been investigated in some molluscs. Hemolymph glucose levels in *A. cygnea, U. pictorum* (Plisetskaya et al. 1978), and *S. oblongus* (Marques and Falkmer 1976) are affected by insulin in ways analogous to those found in mammals. In addition, insulin-like proteins have been reported in several freshwater bivalves (Plisetskaya et al. 1978), a terrestrial snail (Marques and Falkmer 1976), and in saltwater bivalves (Collip 1923, Fritsch and Sprang 1977), including *O. edulis* (DeMartinez et al. 1973).

Hemolymph triacylglycerol levels in two other bivalves were at least 20 times those found in oysters in this study. Triacylglycerol concentration in the hemolymph of the hard clam, *Mercenaria mercenaria* (Linné), was 1 mg/100 mℓ (Hoskin and Hoskin 1977), and in the plasma of the deepsea scallop, *P. magellanicus,* values ranged from 0.1 to 1 mg/100 mℓ (Thompson 1977). The low levels of hemolymph triacylglycerols and free fatty acids in bivalve molluscs may be a consequence of their general metabolic strategy. As facultative anaerobes (Zandee et al. 1980) these animals would be more dependent upon carbohydrate for energy than lipid.

Few reports on the concentration of hemolymph proteins have appeared. Hand and Stickle (1977) examined ninhydrin-positive substances in whole hemolymph from *C. virginica*. Their values ranged from 193 to 702 mg/mℓ; however, those investigators were studying hemolymph which had not been subjected to centrifugation and, in addition, the ninhydrin method detects not only protein but also free amino acids. Thus, the large differences in data from the two laboratories may be explained. On the other hand, plasma from *P. magellanicus* contained LPS in the range of 1.55 to 2.17 mg/mℓ (Thompson 1977).

The different levels of hemolymph glucose and LPS which were observed after the oysters were exposed to several temperature and salinity regimes may reflect adaptive metabolic mechanisms. These adaptive mechanisms would be necessary because oysters are sessile and, thus, subjected to the challenges of a changing euryhaline habitat. For example, successful acclimation to changing ambient salinity is apparently closely related to hemolymph amine concentration. Other investigators have found that hemolymph protein and amino acid levels not only in *C. virginica* (Hand and Stickle 1977), but also in *Pyrazus ebeninus* (Bruguière) (Ivanovici et al. 1981) as well as the tissue free amino acid values (Lynch and Wood 1966), vary directly with ambient salinity. This phenomenon was readily observed with ambient salinity changes of $\geqslant 6$ ppt provided that the animals had been acclimated to the particular salinity for a period of at least two weeks. This is the first report that hemolymph glucose levels also vary with ambient salinity.

Temperature also affects the metabolism of bivalve molluscs. Oysters that are held at elevated temperatures have increased metabolic rates as measured by increased oxygen utilization (Percy and Aldrich 1971, Percy et al. 1971, Shumway and Koehn 1981). As ambient temperature increases, oyster hemolymph glucose levels decrease. Similarly short-term exposure (30 to 60 hours) of *Mytilus galloprovinciallus* Lamarck to elevated temperature regimes caused a decrease in hemolymph glucose (Madar et al. 1980). The physiological importance of these findings remains to be explored.

ACKNOWLEDGMENTS

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EFFECT OF RATION ON GROWTH AND GROWTH EFFICIENCY
OF JUVENILES OF *CRASSOSTREA VIRGINICA* (GMELIN)

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ABSTRACT   Juveniles of *Crassostrea virginica* were batch-fed on different rations of an algal diet of *Thalassiosira pseudonana* and *Isochrysis* aff. *galbana* in experiments lasting three weeks and the resulting growth and growth efficiencies were determined. Maximum growth occurred when the oysters were fed on the highest daily ration tested which was equal, at the beginning of an experiment, to an algal dry weight of 4.6% of oyster live weight. Weight-specific rations decreased during each week of growth experiments because rations were only adjusted for oyster growth on a weekly basis. An initial daily ration of 4.6% was calculated to be equivalent to an effective daily ration of 2.8% of oyster live weight or 59.6% of oyster dry organic weight per week of an experiment. Highest growth efficiencies of 17.9 to 22.6% occurred with effective rations of 1.4 to 2.3% of oyster live weight. The experimental results indicated that weekly adjusted rations based upon previously reported formulae for the prediction of adequate rations for *C. virginica* may not be sufficient in meeting the requirements of juvenile oysters for maximum growth.

KEY WORDS.   ration, oyster, growth, algae, growth efficiency, *Crassostrea virginica*

INTRODUCTION

Successful rearing of bivalve molluscs for both research and commercial purposes depends upon the delivery of an adequate food ration. Despite many attempts to develop satisfactory nonalgal diets or supplements (e.g., Chanley and Normandin 1967, Winter 1974, Masson 1977, Epifanio 1979), algae remain indispensable as the principle food source for artificially reared bivalves. Growth studies have resulted in the determination of the relative food qualities of different algal species (for reviews see Epifanio [1983] and Webb and Chu [1983]); however, the relationship between ration size and bivalve growth rate has not been adequately studied for many bivalve species.

The most complete studies on the relationship between ration size and growth of bivalves were conducted by Bayne and co-workers with *Mytilus edulis* L. (Bayne 1976, Widdows 1978a,b), and Navarro and Winter (1982) for *Mytilus chilensis* Hubé. On the basis of measurements of the energy balance of *Mytilus* spp. fed on a range of algal rations under different conditions of algal cell density and animal body weight, numerical relationships were formulated that integrated these variables in a predictive model of "scope for growth." Scope for growth can be defined as the energy of the assimilated ration available for somatic and/or germinal tissue growth, once metabolic energy requirements have been met (Warren and Davies 1967). Bayne and Worall (1980) and Navarro and Winter (1982) found close agreement between growth of mussel populations in the field and growth predicted by such mathematical models. Less is known about the interrelationships among ration, metabolism, and growth for oysters, although assimilation and growth efficiences of *Crassostrea virginica* (Gmelin) have been reported by several workers (Tenore and Dunstan

1973, Langfoss and Maurer 1975, Romberger and Epifanio 1981, Valenti and Epifanio 1981).

Predicting optimum algal rations for maximum oyster growth on the basis of caloric measurements and scope for growth determinations is of limited practical usefulness because algal diets vary in their nutritive value (Epifanio 1983, Webb and Chu 1983); thus, an algal ration may be calorifically satisfactory but biochemically deficient in some essential nutrient for growth. Because factors determining algal food value are not fully understood, optimum rations for maximum oyster growth must be determined empirically.

In this study, the effect of algal ration on the growth and gross growth efficiency of juveniles of *C. virginica* was determined. The tested rations were compared with the predicted rations for maximum oyster growth described by Epifanio and Ewart (1977), Pruder et al. (1977), and Epifanio (1979).

MATERIALS AND METHODS

Juveniles of *C. virginica* were fed different algal rations in a series of four experiments. In each experiment, groups of 20 oysters were randomly chosen from a population of similar sized oysters. Initial oyster live weight did not vary by more than one standard deviation of the population mean live weight. The identities of individual oysters were maintained during growth experiments by partitioning the oysters in 400 μm mesh trays, which were submerged in 4 ℓ of 1-μm-filtered seawater at 30 ppt salinity and 25°C. The cultures were aerated to keep the algal cells in suspension and the seawater was changed daily.

The animals were fed rations composed of a 50/50 mixture (based on dry weight [wt]) of *Thalassiosira pseudonana*

Hasle and Heimdal (clone 3H) and *Isochrysis* aff. *galbana* Parke (clone T-ISO). This algal mixture supports excellent growth of juveniles of *C. virginica* (Ewart and Epifanio 1981). The algae were cultured in 250-ℓ containers at 19°C, illuminated with 550-600 μW/cm^2 of light (cool white fluorescent lamps), and nutrient enriched with f/2 medium (Guillard 1975). Algal cell dry weights were assumed to be 1.32×10^{-8} mg/cell for *T. pseudonana* (Epifanio and Ewart 1977) and 2.01×10^{-8} mg/cell for *I.* aff. *galbana* (S. Ali, University of Khartoum, Port Sudan, Sudan, pers. comm.). Algal concentrations were determined using a hemocytometer.

Initial algal rations that ranged in dry algal weight from 0.52 to 4.6% of oyster live weight were tested in growth experiments (Table 1). Algal concentrations ranged from 0.12 mg dry wt algae/ℓ (10,000 cells/mℓ) to 2.60 mg dry wt algae/ℓ (217,000 cells/mℓ) (Table 1). By adding one-half the algal ration twice a day to the 4-ℓ culture vessels, it was possible to feed oysters algal cell concentrations which never exceeded 500,000 cells mℓ$^{-1}$, and, therefore, were less than concentrations reported to cause pseudofecal production in *C. virginica* (Epifanio and Ewart 1977). Clearance of algal cells was greater than 95% per day in all treatments and, therefore, little loss of ration occurred.

Oysters were weighed individually at the beginning of each experiment. Group live weights were used for weekly adjustments of rations to compensate for oyster growth during each week of the experiment. At the end of the

experiments, oysters were reweighed individually, dried to constant weight at 60°C, weighed, and then ashed at 450°C for 24 to 48 hours and reweighed (Walne and Millican 1978). The difference between total dry weight and ash weight was assumed to be equal to total oyster organic weight. Individual live, dry, ash, and organic weights were similarly determined for an initial sample of 50 oysters at the beginning of each experiment.

RESULTS

The weight-specific daily rations decreased during each week of an experiment as a result of the growth of the animals and because the rations were only adjusted weekly (Figure 1). This decrease was greatest in treatments with rapidly growing oysters. To obtain a better estimate of the effective ration fed to the oysters, the geometric mean of the actual daily ration was determined for each week of an experiment. The overall effective ration for the 3-week experiment was calculated as the mean weekly effective ration (Table 1).

Oyster growth rate increased with increasing effective ration over the range tested of 0.2 to 2.8% of oyster live weight (Table 1 and Figure 2). The highest effective algal ration of 2.8% of oyster live weight was equivalent to a ration of 59.6% of oyster dry organic weight, based on a mean dry organic content of 4.7% for oysters from two experiments (Table 2). Regression analysis of log-transformed,

TABLE 1.

Initial, final, and effective percent rations and the resulting growth
of juveniles of *Crassostrea virginica* after 3 weeks.

Initial Ration Concentration (mg dry wt algae ℓ$^{-1}$)	Percent Rations*			k Value†	Percent Increase in Oyster Live Wt
	Initial	Final	Effective		
2.60	4.6	1.9	2.8	0.128	1363
2.60	4.6	1.9	2.8	0.123	1226
1.95	3.5	1.6	2.3	0.107	847
2.60	3.3	1.7	2.2	0.098	687
1.30	2.3	1.2	1.6	0.093	604
1.30	2.3	1.2	1.6	0.091	585
0.97	1.7	1.0	1.2	0.070	338
2.60	1.9	1.2	1.4	0.067	305
0.65	1.2	0.8	0.9	0.057	231
1.95	1.4	1.0	1.1	0.053	203
0.65	1.2	0.8	1.0	0.049	183
0.65	0.8	0.6	0.6	0.037	120
1.30	0.9	0.7	0.7	0.037	107
0.32	0.6	0.5	0.5	0.027	78
0.65	0.5	0.4	0.4	0.018	45
0.12	0.2	0.2	0.2	0.013	31
unfed	0.0	0.0	0.0	0.009	22‡
unfed	0.0	0.0	0.0	0.005	10‡
unfed	0.0	0.0	0.0	0.003	6‡

*Percent ration = ([dry wt of algae per oyster live wt] $\times$ 100). Effective ration is the geometric mean ration for each week, averaged for the 3-week experiment (Figure 1).

†k is the daily instantaneous relative growth rate (see RESULTS for formula).

‡Live weight increases of unfed oysters probably resulted from increases in inorganic shell weight because the organic content of unfed oysters decreased during the experiment (Table 2).

weekly live-oyster weights plotted against time, indicated that growth occurred at a constant exponential rate for oysters fed on the 2.8% effective ration ($r^2 = 0.997$, $F_{(1,6)} = 2615.3$, $p < 0.001$).
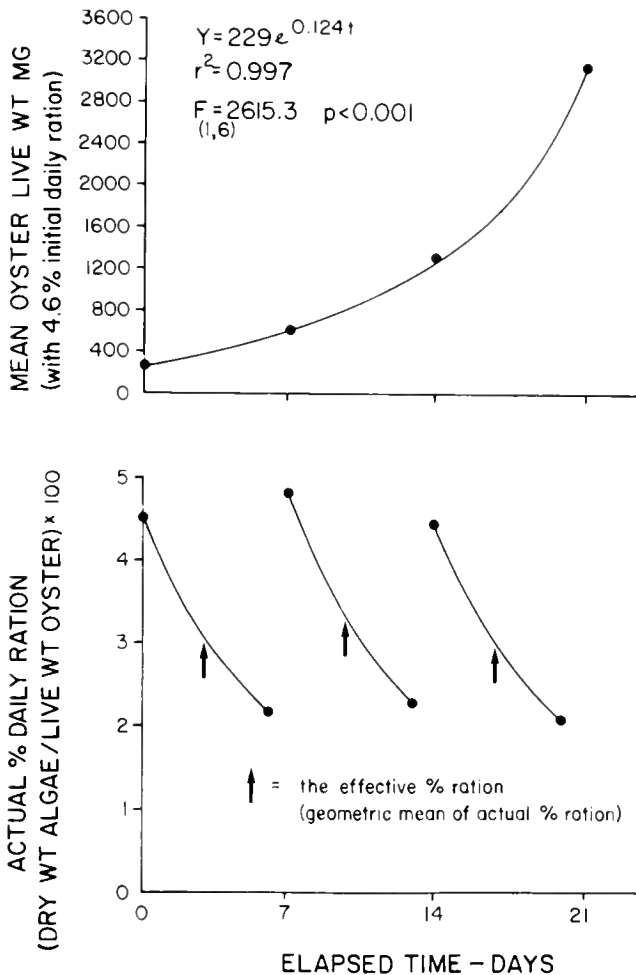

Figure 1. Change in percent daily ration for *Crassostrea virginica* fed an initial daily ration of 4.6%. The upper curve shows the growth of juveniles of *C. virginica* fed an initial daily ration of 4.6% over a 3-week period. The lower figure shows the change in the percent daily ration over the course of each week of the experiment. The vertical arrow indicates the effective ration for each week. The t-value in the exponential equation is in days.

The daily instantaneous relative growth rate (k) was calculated for each ration (Table 1), where

$$k = [(dWt/dt)/Wo] = (2.303/t) \log (Wt/Wo)$$

and Wo is the initial live weight (mg) and Wt is the final live weight (mg) after 21 days (t) of growth (Brody 1945). The k values and values for percentage increase in oyster live weight were both directly dependent on the weight-specific ration and were not greatly affected by the concentration of algae added to obtain the required ration (Table 1).
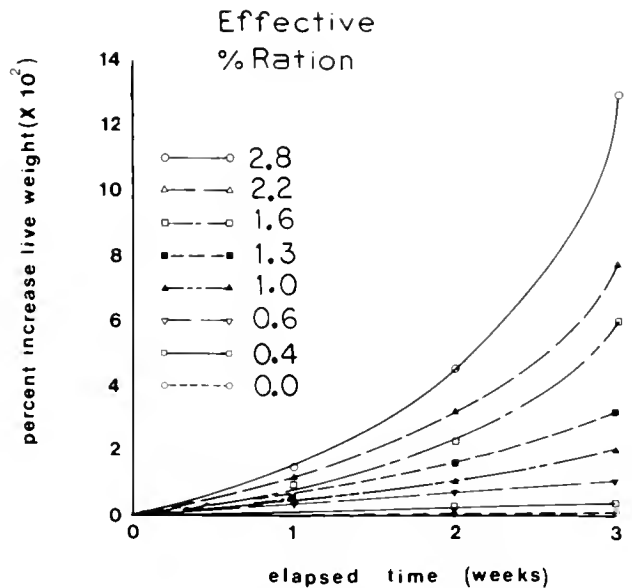
Figure 2. Increase in live weight of juveniles of *Crassostrea virginica* fed different effective percent rations of an algal diet of *Thalassiosira pseudonana* and *Isochrysis* aff. *galbana*. Percent increase in live weight was calculated from initial live weight.

Table 2 and Figure 3 give gross growth efficiencies for oysters fed different rations. Figure 3 shows that gross growth efficiency increased from -37.7% at an effective ration of 0.2% to a maximum of 22.6% with an effective ration of 1.4%. Gross growth efficiency declined slightly as rations were increased from 1.6 to 2.8%. From Figure 3, the maintenance ration for juvenile oysters cultured under the described conditions was 0.5% of oyster live weight. The organic content of both starved oysters and oysters fed a 0.2% effective ration decreased over the experimental period, compared with initial samples. Increases in total dry weights of starved oysters and oysters fed a 0.2% effective ration resulted, therefore, from increases in ash content, probably as a result of shell growth.

DISCUSSION

In bivalve growth experiments carried out by Langton and McKay (1975) and Gallager and Mann (1981), ration was not adjusted according to growth over the entire experimental period and the animals were fed a constant amount of food per individual. An important consequence of maintaining a constant ration with rapidly growing animals is that the weight-specific ration (expressed as a percentage of oyster live weight in this study) decreases as the animal grows (Figure 1). An example of large decreases in weight-specific ration is evident in Experiment 6 of Walne and Spencer (1974) in which a ration of *Tetraselmis suecica* (Kylin) Butch. fed to *Ostrea edulis* Linné decreased from 35 to 2% of oyster live weight over a 3-week period. This occurred even though the authors attempted to compensate for oyster growth by limited, but insufficient,

TABLE 2.

The relationship between the effective algal ration and the resulting growth
and gross growth efficiency of juveniles of *Crassostrea virginica.*

Effective Ration* (× 100)	Initial Oyster Live Wt (mg)	Increase in Oyster Live Wt (mg)	Increase in Oyster Dry Organic Wt (mg)	Final Oyster Organic Dry Wt/Live Wt	Dry Wt of Algae fed per Experiment (mg)	Percent Increase in Oyster Live Wt/ Dry Wt of Algae fed per Experiment	Gross Growth Efficiency† (GGE)
2.8	224.76	3,014.3	151.12	0.051	715.5	420	21.1
2.8	228.17	2,774.2	114.48	0.043	615.2	450	18.6
2.2	315.78	2,135.6	85.30	0.040	475.7	450	17.9
2.3	221.60	1,853.7	75.25	0.043	383.6	480	19.4
1.6	224.64	1,265.0	46.88	0.041	231.1	550	20.3
1.6	225.43	1,337.8	48.08	0.040	271.5	610	22.1
1.2	227.85	723.0	28.42	0.044	143.4	500	19.8
1.4	557.65	1,671.7	78.77	0.046	347.4	480	22.6
1.0	224.96	362.4	38.34	0.085‡	82.2	440	46.6‡
1.1	556.17	1,098.8	46.07	0.042	224.3	490	20.5
0.9	222.00	490.4	15.50	0.043	77.7	630	19.9
0.7	559.33	628.5	26.30	0.042	133.4	470	19.7
0.6	316.69	344.3	12.34	0.039	65.0	530	19.0
0.5	224.91	126.8	0.13	0.040	24.0	370	0.5
0.2	228.22	47.0	− 4.22	0.039	11.2	420	−37.7
0.4	556.11	219.7	6.35	0.038	57.2	380	11.1
unfed	219.17	48.2★	− 5.86	0.037	–––	––	–––
unfed	220.73	22.7★	− 6.43	0.039	–––	––	–––
unfed	551.66	31.9★	− 2.58	0.038	–––	––	–––

*Effective percent ration = average weekly effective percent ration for a 3-week experiment (Figure 1), expressed as (mg dry wt algae per mg live wt oyster) × 100.

†Gross growth efficiency (GGE) = (increase in oyster dry organic weight/total dry weight of algae fed) × 100 for an experimental period of 3 weeks.

‡These values are anomalous and may have resulted from analytical error.

★Increases in the live weight of fed animals were adjusted by subtracting the mean increase in the live weight of starved animals. This was necessary to accurately determine gross growth efficiency (Winberg 1958).

weekly increases in ration. Clearly, if a constant weight-specific ration is desired throughout a growth experiment, frequent adjustments of ration in proportion to bivalve growth are necessary. Such adjustments are especially important in growth experiments with juvenile animals in which weight-specific growth rates are high, and which result in significant changes in weight-specific rations over short periods of time, unless frequent ration adjustments are made. Changes in weight-specific rations will be less dramatic with large animals that have lower weight-specific growth rates. Under certain conditions the use of photo-electric devices to maintain constant algal concentrations may be useful (Winter 1973).

Pruder et al. (1976, 1977), Epifanio and Ewart (1977), and Epifanio (1979) attempted to determine the maximum ration that could be ingested by bivalves under optimal growth conditions where excess food was available. Under those conditions, they assumed that the growth rate would be greatest when the animal was fed as much food as it could consume, i.e., a maximum ration (Epifanio and Ewart 1977). Because maximum ration is dependent on animal weight (Navarro and Winter 1982), several ration formulae, derived from measurements of the filtration rates of
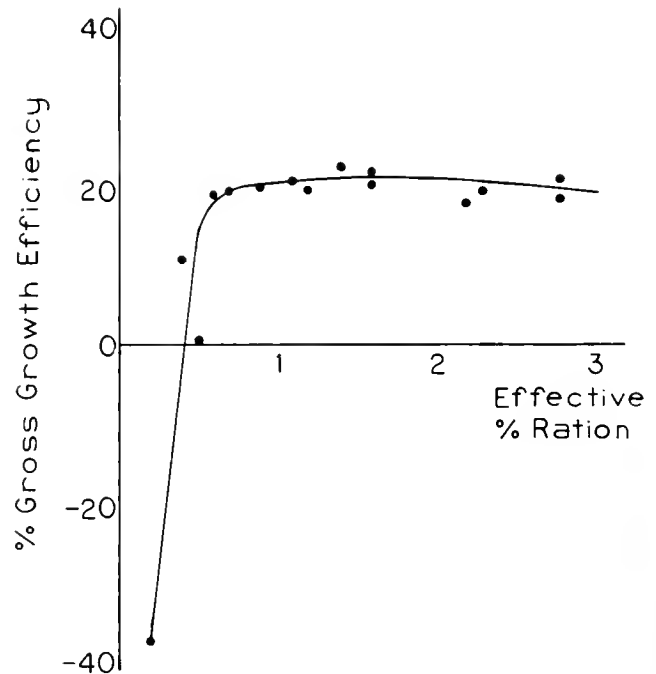

Figure 3. Gross growth efficiencies of juveniles of *C. virginica* fed different effective percent rations for a period of 3 weeks. GGE = (increase in oyster organic dry wt/dry wt of algae fed) × 100.

Crassostrea virginica, have been described in an attempt to predict the maximum ration on a weight-specific basis. Pruder et al. (1976) reported an empirically derived equation relating oyster weight to a daily requirement of cells of a mixture of *Thalassiosira pseudonana* and *Isochrysis galbana*. The equation $Y = 5.3 W^{-0.41}$ was derived on the basis of the maximum filtration rates of both laboratory-reared juvenile oysters and adult oysters from the field, where Y was the daily ration of algal cells of a 50/50 mixture (by cell number) of *T. pseudonana* and *I. galbana* $\times 10^8$ per gram live weight of oyster and W was the individual oyster live weight in grams. Later, Pruder et al. (1977) repeated the work using only laboratory-reared oysters and the equation was modified to $Y = 8.2 W^{-0.21}$. The modification was required because laboratory-reared oysters had a higher content of organic material compared with wild oysters.

Epifanio and Ewart (1977) determined the maximum dry weights of four algal species which could be filtered from suspension by laboratory-reared oysters (*C. virginica*) of 15 g live weight. They found that the maximum ration cleared varied from 4 mg/g/day (0.4% ration) for *T. pseudonana* to 15 mg/g/day (1.5% ration) for *I. galbana*. Using a maximum ration of 4 mg/g/day and a value for the exponent of −0.41 obtained from Pruder et al. (1976), Epifanio and Ewart (1977) derived the equation $R/W = 0.01 W^{-0.41}$, where R was the daily ration of algae in mg dry weight, and W was the individual live weight of the animal in grams. In a later paper, Epifanio (1979) adjusted the value of the exponent to a theoretical value which was closer to the empirical value of Pruder et al. (1977) and the formula predicting ration size was given as $R/W = 0.01 W^{-0.33}$.

The growth of *C. virginica* fed on rations derived from the formulae of Pruder, Epifanio, and co-workers has not been studied experimentally. In Figure 4, the predicted rations are compared with those of the present study. In the first week, the 4.6% initial ration was lower than the predicted ration of Epifanio and Ewart (1977), but higher than the rations of Pruder et al. (1977) and Epifanio (1979). As the animals grew, the predicted rations based on the weight-specific equations decreased and in the second and third week of the growth experiment, all were less than the 4.6% initial ration used in the present study.

It was impossible to definitely determine which rations given in Figure 4 would support the greatest oyster growth. Juvenile oysters fed on the highest initial ration of 4.6% in this study grew at a constant exponential growth rate throughout the experimental period (Table 1, Figure 1), and were not adversely affected by the high algal concentrations of the ration during the latter part of the experimental period. The optimal ration for maximum growth of juvenile oysters weighing 11 to 64 mg was, therefore, probably greater than that predicted by the weight-specific equations. Further study is necessary to test this hypothesis with juvenile oysters weighing less than 1 g, because the equations of Epifanio and Ewart (1977) and Pruder et al.

(1977) were derived from experiments using larger oysters than those used in the present study.
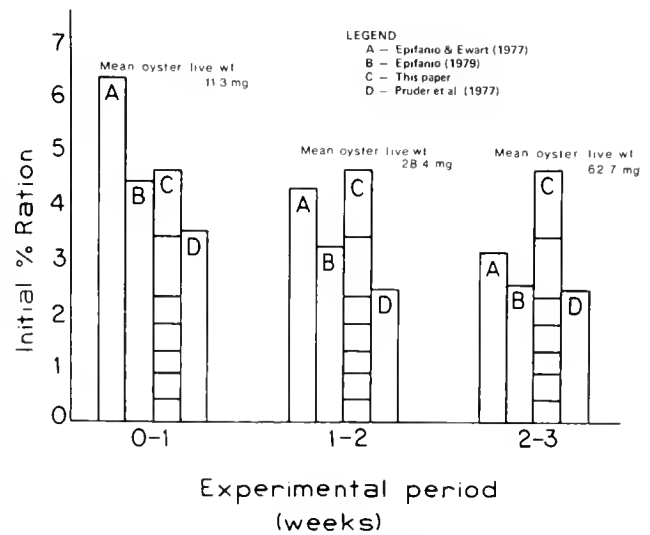

Figure 4. A comparison of the initial percent rations used in the present paper and initial percent rations derived from reported equations for determining the maximum ration for *Crassostrea virginica*. The initial weekly mean individual live weights of oyster fed the 4.6% ration in the present study are indicated above each set of bars. These weights were used to calculate initial percent rations. The 8-part bar "C" indicates the eight rations used in the present study (Table 1).

The relationship between ration size and gross growth efficiency (Figure 3) is similar to that reported for *Mytilus edulis* by Thompson and Bayne (1974) in that there was initially a dramatic increase in gross growth efficiency to a maximum value, followed by a slight decline with further increases in ration. At still higher rations, gross growth efficiency may decrease even more sharply, making it important for commercial oyster culturists to balance the cost savings of further improvements in growth rate with the increased costs of decreased utilization of expensive algal food. Comparisons between gross growth efficiencies of *M. edulis* and those reported in this paper for *C. virginica* are difficult because Thompson and Bayne (1974) used larger animals and also expressed gross growth efficiency in terms of tissue dry organic weight and not total organic weight (i.e., they did not include the contribution of the food to synthesis of the organic fraction of the shell). Price et al. (1976) reported that 39% of the total organic material of *M. edulis* (3.5 to 14.4 g live weight) was present in the shell and that 72% was present in the shell of adults of *C. virginica* (80.9 to 170 g live weight). For juveniles of *C. virginica* (10 to 30 mg live weight), the proportion of the total organic matter present in the shell is 33.8 ± 5.8% (C. Langdon, University of Delaware, Lewes, DE, unpublished data). Clearly, failure to take into account increases in

the organic content of the shell may result in considerable underestimations of gross growth efficiencies (see Jorgensen 1976).

Based on measurements of the total increase in the organic weight of juvenile oysters, Romberger and Epifanio (1981) reported a maximum gross growth efficiency of 36% for *C. virginica* fed a 50/50 mixture (by cell volume) of *T. pseudonana* and *I. galbana* at ration levels based on the predicted rations of Epifanio and Ewart (1977). Their maximum gross growth efficiency was, therefore, greater than the highest efficiency found in this study of 22.6% and may have resulted from differences in culture conditions.

In conclusion, the use of high-algal rations and high concentrations of algae up to 500,000 cells ml^{-1} need not be detrimental to oyster growth or growth efficiency when

used in batch-feeding systems (Pruder and Greenhaugh 1978). The highest initial percentage ration tested in this study of 4.6% was greater than those recommended for oysters of the same size by the predictive equations discussed above. Constant adjustments of ration are required to compensate for increases in oyster weight during the course of growth experiments. An initial daily ration of 4.6%, which was equivalent to an effective daily ration of 2.8% per week, supported good growth of juveniles of *C. virginica* under the conditions of this study. Optimal rations for maximum oyster growth will vary according to culture conditions. Empirical growth studies, such as those described here, are useful because they integrate culture conditions with both the physiological and nutritional requirements of oysters for maximum growth.

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EFFECT OF DEPURATION SYSTEMS ON THE REDUCTION OF BACTERIOLOGICAL INDICATORS IN CULTURED MUSSELS (*MYTILUS EDULIS* LINNAEUS)

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ABSTRACT   Five bacteriological parameters (total coliforms, fecal coliforms, fecal streptococci, *Escherichia coli*, and total viable count) were used to examine depuration of cultured mussels (*Mytilus edulis* Linnaeus) by two different systems, one using chlorine as a disinfection agent for the water, and the other using untreated seawater. The most significant difference in post-depuration levels between chlorinated and untreated seawater systems was obtained for fecal coliforms (63.4 and 90.1% reduction, respectively), whereas reduction of the other bacteriological parameters were quite similar for both depuration methods. Although there was a large decrease in the fecal streptococci ($> 74\%$), high residual numbers could be detected after depuration. From the identification of bacteria isolated from mussels, we found that the pathogens *Salmonella* and *Yersinia* were not recovered in the depurated samples, even though the genera *Citrobacter, Enterobacter,* and *Escherichia coli* were detected either before or after depuration. The drug-resistance patterns of the most representative members of the enterobacteria isolated from mussels were also determined.

KEY WORDS: mussels, *Mytilus edulis*, shellfish depuration, pollution indicators, drug-resistance

INTRODUCTION

Since Dogson (1928) found that depuration was an effective method for reducing the microbial flora of contaminated shellfish, this method has been adopted as the best technique for reducing the potential risk of public health hazards associated with the consumption of shellfish which might have accumulated high levels of bacterial or viral pathogens.

In Galician "rías" (Atlantic coast of northwestern Spain), the production of cultured mussels (*Mytilus edulis* Linnaeus) on rafts is a very important economic activity, reaching 200,000 metric tonnes in 1981. Approximately 50% of this production is destined for daily consumption and export, following depuration which is required by Spanish regulations.

The depuration process is based on holding shellfish in tanks containing seawater that has been sterilized by physical or chemical means. The technology of depuration has been well studied (Huntley and Hammerstrom 1971, Neilson et al. 1978, Souness et al. 1979), and reviewed (Furfari 1976, Fleet 1978). Most countries have chosen to clean their shellfish in depuration plants rather than by relaying in natural waterways. Ultraviolet irradiation, ozonation, and chlorination are widely used to sterilize seawater for depuration (Kelly 1961, Wood 1961, Anon. 1972); however, Reynolds (1956) showed that the process could be simplified if depuration plants were located in areas with light or no contamination. In the former cases, the water sterilization step could be suppressed. Because of the special geography of Galician rías, it is possible to find within 30 km (18 miles) depuration plants located in areas

without microbial contamination, as well as others, nearer populated areas (on the middle upper part), that must use disinfection agents for water treatment.

Our objective was to compare the reduction of bacteriological indicators of pollution in cultured mussels which were subjected to depuration systems that used either chlorinated seawater or untreated seawater.

MATERIAL AND METHODS

The sampling area selected for this study is located in northwestern Spain (Figure 1). Mussel samples were collected from January to June 1982, from rafts located in several shellfish-growing areas, and were treated in three different depuration plants; two plants used chlorinated seawater and the other used untreated seawater.

During the sampling period, the water salinity ranged from 31.7 to 34.3 ppt and the temperature oscillated between 13 and 19°C. Total coliform levels of the water in the chlorine-treated systems ranged from 230 to 830 per 100 mℓ. The standard dose of chlorine for water treatment was 3 ppm. Treated water was dechlorinated by an appropriate aeration period before the mussels were placed into the shellfish tanks. In the untreated system, the detected level of total coliforms was never higher than 9/100 mℓ. In both the treated and untreated systems the depuration time period was 48 hours.

Samples were taken twice a month before and after depuration, transported to the laboratory in isotherm containers, and immediately processed. Each sample was divided into two subsamples which were analyzed simultaneously. Mussels were shucked aseptically according to
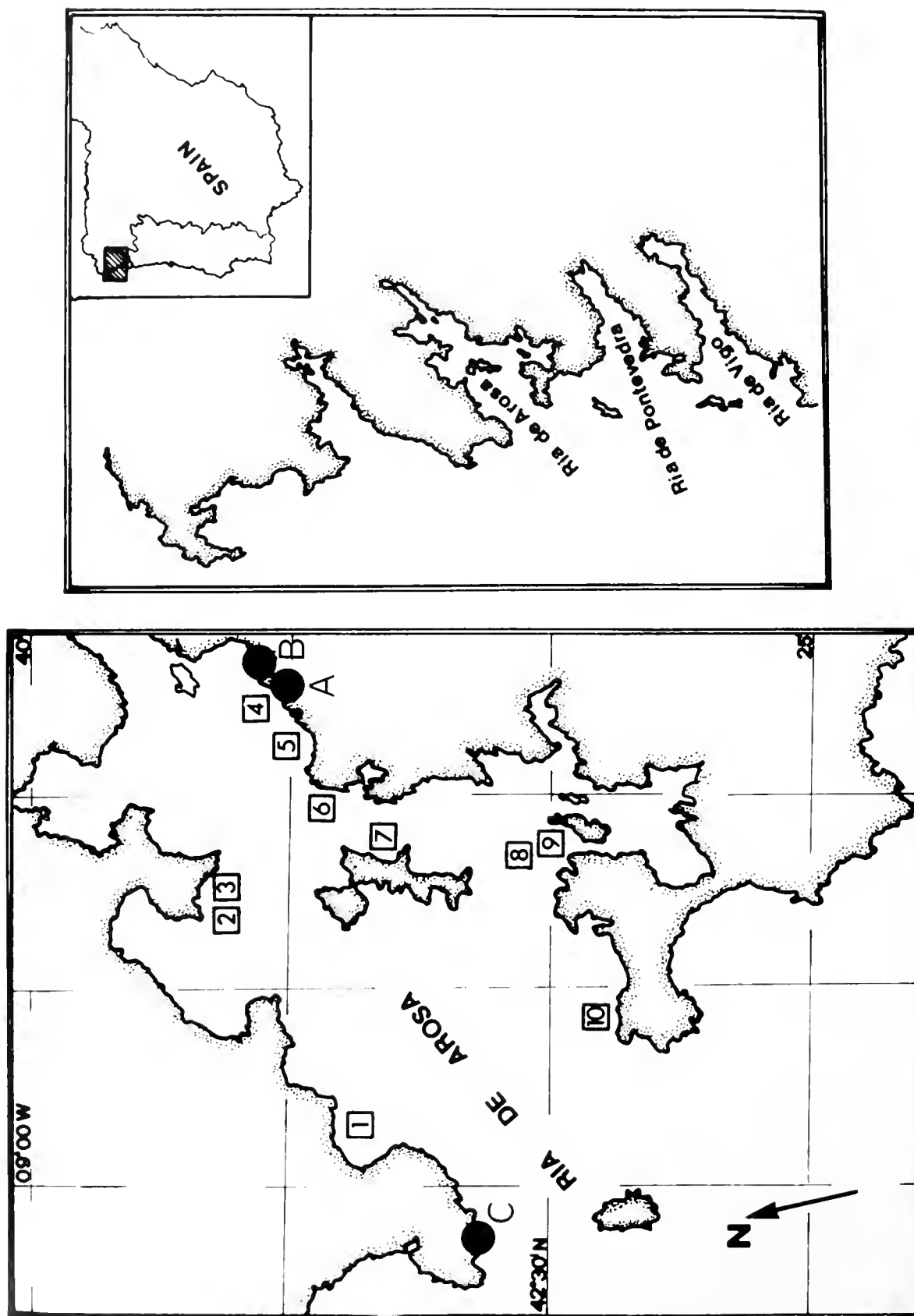
Figure 1. Location of the sampling area. Numbers indicate the shellfish growing areas. Letters correspond to the shellfish depuration plants (A and B, using chlorine; C, using untreated seawater).

procedures recommended for shellfish by the American Public Health Association (APHA 1970). One hundred grams (100 g) of shellfish meat without mantle fluid (corresponding to six mussels) were weighed aseptically. After the addition of 1% of peptone water, the mixture (1:9 w/v) was homogenized for 60 seconds in a sterile Waring blender. Each homogenate was transferred into a sterile flask and used as inoculum. Ten-fold serial dilutions of the homogenate were inoculated in triplicate on plate-count agar (Difco) and incubated at 37°C for 24 hours. After incubation, plates were counted and the results were expressed as colony-forming units (CFU) per gram.

Total coliforms were estimated by the standard most probable number (MPN) method using three dilutions in three tube replication of lactose broth (LB) (Difco). Tubes were incubated at 35°C for 48 hours after which they were examined for growth and gas production (APHA 1970). Lactose broth tubes were reinoculated simultaneously into brilliant-green lactose bile broth (BGLB) (Difco) and into 1% triptone water, then incubated in a water bath at 44.5 ± 0.2°C for the indol test.

Tubes showing growth and gas in BGLB were confirmed as fecal coliforms (FC). The MPN of *Escherichia coli* was determined from positive tubes for both tests, growth with gas at 44.5 ± 0.2°C and indol production.

Fecal streptococci were determined by the MPN method in azide dextrose broth (Difco) at 35°C. Positive tubes of presumptive test were inoculated in ethylviolet-azide broth (Difco) at 35°C. Tubes showing violet sediment were considered positives and the presence of fecal streptococci was confirmed by streaking on KF-streptococcus agar (Difco).

Positive tubes from LB and BGLB of the MPN test were streaked on Levine-eosin methylene blue agar (Difco) and incubated at 37°C for 24 hours to isolate enterobacteria. Colonies were picked randomly from the plates, subcultured repeatedly to obtain pure cultures, and stored on agar slopes under mineral oil at room temperature. The isolates were subjected to taxonomic analysis using morphological, physiological and biochemical tests according to the procedures of Edwards and Ewing (1972) and Bergey's Manual (Buchanan and Gibbons 1974).

The drug-resistance patterns of the isolates were determined by the diffusion disk assay method of Bauer et al. (1966) on Mueller-Hinton agar (Difco). The following antibiotics and concentrations were used: ampicillin (10 μg), chloramphenicol (30 μg), erythromycin (15 μg), gentamicin (10 μg), polymyxin B (300 units), nalidixic acid (30 μg), kanamycin (30 μg), tetracycline (30 μg), and streptomycin (10 μg).

RESULTS AND DISCUSSION

The results obtained in this study of depuration levels of total coliforms (TC), fecal coliforms (FC), fecal streptococci (FS), *Escherichia coli*, and total viable count (TVC) with the two systems used are shown in Table 1 and Figure 2.

In general, only small differences were observed between the two depuration systems. For the total viable count, similar values were obtained. The TVC decreased by 10-fold over the depuration time, but rarely went below values of 10^3 to 10^4 CFU/g of mussel. Similar results were found by Lee and Pfeifer (1974) who worked with oysters depurated by ultraviolet irradiated seawater and, as they indicated, that reduction in bacterial count in shellfish could have been due to the persistance of a stable population of microorganisms in the mussels. In addition, Thi Son and Fleet (1980) obtained even lower reduction levels than ours in a laboratory depuration system with artificially contaminated oysters.

TABLE 1.

Comparison between the reduction levels of bacterial pollution indicators in *Mytilus edulis* obtained in two different depuration systems.

Bacterial Indicators	Percent Reduction in Systems Using	
	Chlorinated Sea Water	Untreated Sea Water
Total viable counts*	61.5	65.5
Total coliforms†	30.2	38.6
Fecal coliforms†	63.4	90.1
Escherichia coli†	91.5	89.0
Fecal streptococci†	74.0	87.0

*Determined on plate-count agar medium at 37°C and expressed as bacterial numbers per gram.
†Determined by the most probable number (MPN) method and expressed as MPN/100 g.

The most important different in the observed depuration in chlorinated and untreated seawater systems was obtained for FC, although in both methods most (about 90%) of this bacterial flora was represented by *E. coli*. The high depuration levels found for this organism agreed with the the results obtained by Thi Son and Fleet (1980) who attained depuration reductions greater than 97%.

Considering only the reduction rates for *E. coli*, we found residual counts to be within the values allowed by Spanish regulation (500 *E. coli*/ℓ) in both depuration systems. If, however, we consider other regulations that use the number of FC as the indicator for bacteriological control, then the untreated seawater system appeared to be the most efficient method (Table 1). The FC levels in this system after depuration were below the recommended wholesale level of ≤ 230/100 g (Slalyj 1980) suggested by the U.S. National Shellfish Sanitation Program for naturally harvested shellfish.

Examination of bacteria isolated from mussels showed that the genera *Citrobacter*, *Enterobacter* and *Escherichia coli* were detected before and after depuration whereas other pathogens or potential pathogens such as *Salmonella* and *Yersinia* were not isolated from depurated samples of mussels (Figure 3). The elimination of organisms such as
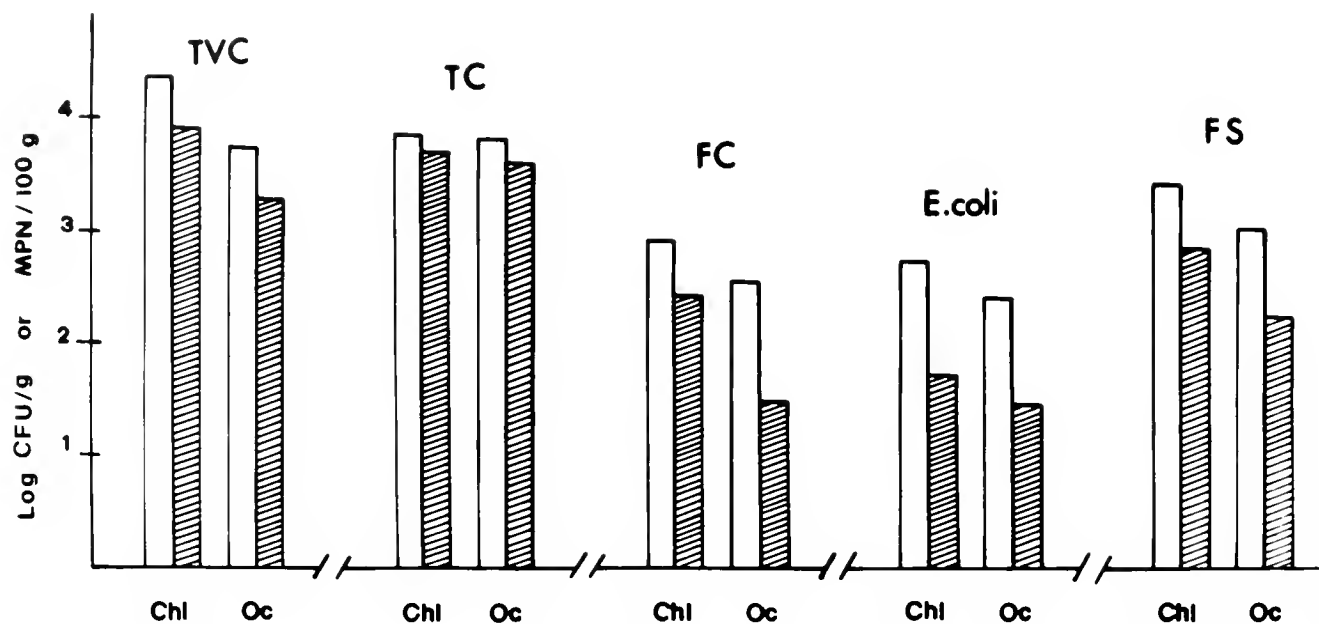
Figure 2. Comparison between the reduction rates of bacteriological indicators obtained by the two different methods employed.
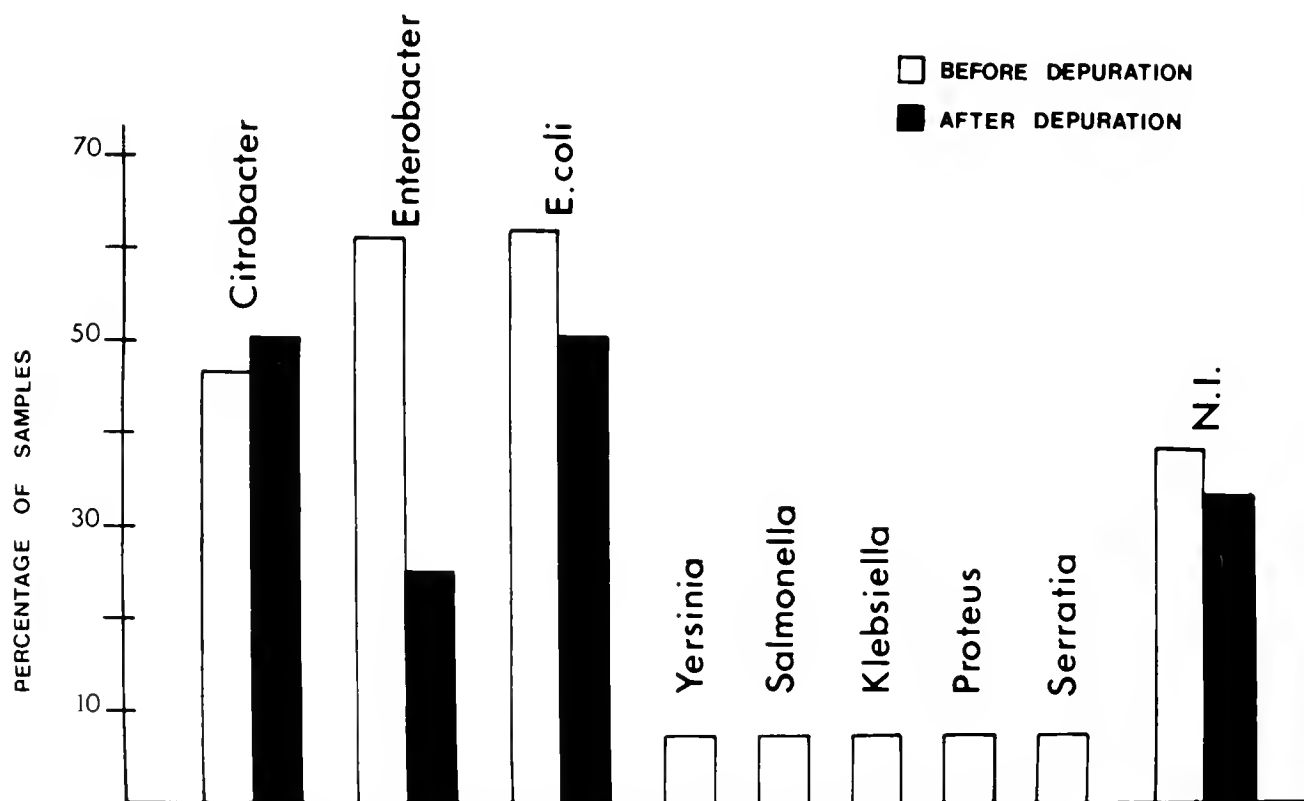

Figure 3. Distribution of bacteria obtained from mussels before and after depuration.

Salmonella sp., *Vibrio parahaemolyticus*, and other pathogens during 48-hour depuration periods was also demonstrated by Metcalf et al. (1973) and Thi Son and Fleet (1980).

Although the reduction levels obtained for FS were similar in both systems (Table 1), very high numbers of these bacteria were present in mussels before and after depuration. This result supports the described higher survival of FS with respect to other bacteriological indicators in the marine environment (Cohen and Shuval 1972, Anson and Ware 1974).

We determined the sensitivity of the enterobacteria isolated from mussels to antibiotics and chemotherapeutic agents; 77% of the strains displayed resistance to two or more antibiotics. Table 2 shows the resistance patterns of the most representative members of enterobacteria isolated: *E. coli*, *Citrobacter*, and *Enterobacter–Klebsiella* group. The percentage of *E. coli* strains resistant to tetracycline was 44.5%, with the most frequent pattern being erythromycin-tetracycline resistance. Most (90.8%) of the *Citrobacter* strains were resistant to streptomycin, showing as predominant resistance pattern erytromycin-streptomycin. Of the isolates belonging to the *Enterobacter–Klebsiella* group, 69.2% were resistant to ampicillin, with the predominant pattern erythromycin-ampicillin.

Resistance to polymyxin and nalidixic acid was found only in the genus *Citrobacter*, whereas resistance to chloramphenicol, gentamicin, and kanamycin was present only in *E. coli* and *Enterobacter–Klebsiella* group strains, associated with multi-resistant patterns.

It has been demonstrated that plasmids present in enterobacteria codify drug resistance (Stewart and Koditscheck 1980), as well as a variety of characteristics like virulence (Elwell and Shipley 1980, Gemski et al. 1980, Jones et al. 1982), enterotoxin production (Gyles et al. 1974, 1977; Mazaitis et al. 1981), and metabolic properties such as urease production and citrate utilization (Gavini et al. 1981), which could explain the relatively high number of unidentified strains found in our study (Figure 3). Work in progress indicates that these strains are multiplasmidic and preliminary results have been presented (Barja et al. 1982).

TABLE 2.

Resistance patterns at two or more antibiotics in the most representative members of enterobacteria isolated from *Mytilus edulis.*

Bacterial Strains	Resistance Patterns*	Percentage
Escherichia coli	E Te	36.1
(36 strains)†	E S	8.3
	E Am	2.8
	E S Te	2.8
	E S C Am	2.8
	E Te C Am	2.8
	E S Te C K Gm Am	2.8
Citrobacter	E S	50.0
(22 strains)†	E Am	4.5
	E S Te	18.2
	E S Am	13.6
	E S Na	4.5
	E S Pb	4.5
	E Te Pb	4.5
Enterobacter–Klebsiella	E S	18.7
(16 strains)†	E Am	43.7
	E Am Te	12.5
	E S Te Am	6.5
	E S Te C K Gm Am	6.5

*E, erythromycin; Te, tetracycline; S, streptomycin; Am, ampicillin; C, chloramphenicol; K, kanamycin; Gm, gentamicin; Na, nalidixic acid; Pb, polymyxim.
†Number of strains tested.

ACKNOWLEDGMENTS

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DOCUMENTATION AND IMPLICATIONS OF RAPID SUCCESSIVE GAMETOGENIC CYCLES AND BROODS IN THE SHIPWORM *LYRODUS FLORIDANUS* (BARTSCH) (BIVALVIA, TEREDINIDAE)

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ABSTRACT   A pair (male and female) of the shipworm *Lyrodus floridanus* (Bartsch) was removed from the wood and observed over a period of 39 days. The female of this short-term larviparious species broods its larvae in its gills to the straight-hinge stage and then releases them en masse. Gametogenic cycles and brood periods were concurrent and regular, averaging 6.12 (N = 4) and 5.02 (N = 5) days in length, respectively. Problems associated with observing gametogenic cycles and brood periods in single animals, as well as the importance of such data in life-history studies, are discussed. Life history data on *L. floridanus* support its removal from the synonymy of *L. pedicellatus* and establish it as a distinct species.

KEY WORDS: Teredinidae, *Lyrodus*, brooding, gametogenic cycles, veliger larvae, spawning, reproductive cycles, Bivalvia

INTRODUCTION

Lyrodus floridanus (Bartsch), a species of wood-boring bivalve, is found in Florida and probably throughout the Caribbean. It is closely related to the common Californian, but probably widely distributed, *Lyrodus pedicellatus* (Quatrefages) and, generally, cannot be distinguished from that species on the basis of shells and pallets (Turner 1966, Turner and Johnson 1971). While studying the reproductive biology of *L. pedicellatus,* a long-term brooder that releases its larvae in the pediveliger stage, we found that specimens from Florida differed by releasing their larvae in the straight-hinge stage (i.e., they were short-term brooders). This was first noted by Turner and Johnson (1971), but at that time it was thought that under stressed conditions *L. pedicellatus* might release straight-hinge larvae. We now realize that *L. floridanus* is a distinct species with a reproductive pattern like that of *Teredo navalis* Linnaeus. In both of these species, eggs are spawned into the suprabranchial cavity and passed into the water tubes of the gills where they develop to the straight-hinge stage. They are then released en masse and complete their development to the pediveliger stage in the plankton.

To compare fecundities of different species, in this case, *L. pedicellatus* and *L. floridanus,* it is necessary to know the number and sizes of gametogenic cycles (oviparous and brooding species) or broods (brooding species) for individual specimens. Observations of this type were made using a pair (male and female) of *L. floridanus* and form the basis of this paper.

MATERIALS AND METHODS

Animals used in this study were obtained from collecting panels exposed in the intracoastal waterway at Pompano Beach, Florida, from 26 October 1978 to 26 February 1979. Panels were hand-carried to Harvard University, Cambridge,

Massachusetts, on 27 February, and placed in an Instant Ocean aquarium with natural sea water at 19 to 20°C and 32 ppt. They were dissected on the evening of 27 February (day 1) and two uninjured specimens, one male and one female, of *Lyrodus floridanus* (Bartsch), the predominant species found in the panels, were placed in a finger bowl with 200 mℓ of 0.22-μm filtered sea water and maintained in an illuminated incubator at 19 to 20°C. The water and the bowl were changed daily to prevent the build up of bacteria. Because some shipworms are capable of supplementing their diet of wood with phytoplankton (Dean and Back 1979, Pechenik et al. 1979), the animals were fed *Isochrysis galbana*, a naked flagellate, after each water change at a final concentration of 4×10^4 cells/mℓ. Observations on the condition of the gonads and gills of the female were made at each water change and often at shorter intervals to determine the time of spawning and larval release. Although spawning of the male was not observed nor was any obvious change in size of the gonads evident, sperm were seen attached to eggs aborted by the female. When the experiment was terminated upon the death of the female on day 39, gonadal smears of both animals were examined and their sexes confirmed.

RESULTS

Shipworms are good animals for an observational study of this type because the visceral mass, pericardium, gonads and gills, which are located posteriorly to the shell, are clearly visible through the translucent mantle (Figures 1–4). Once the animal is removed from the wood, it is possible to observe development of the gonads and growth of the larvae without disturbing the animal. The gonads are located between the pericardium and the wood-storing caecum, and the genital ducts open into the suprabranchial cavity posteriorly to the visceral ganglion (Figures 1–4).
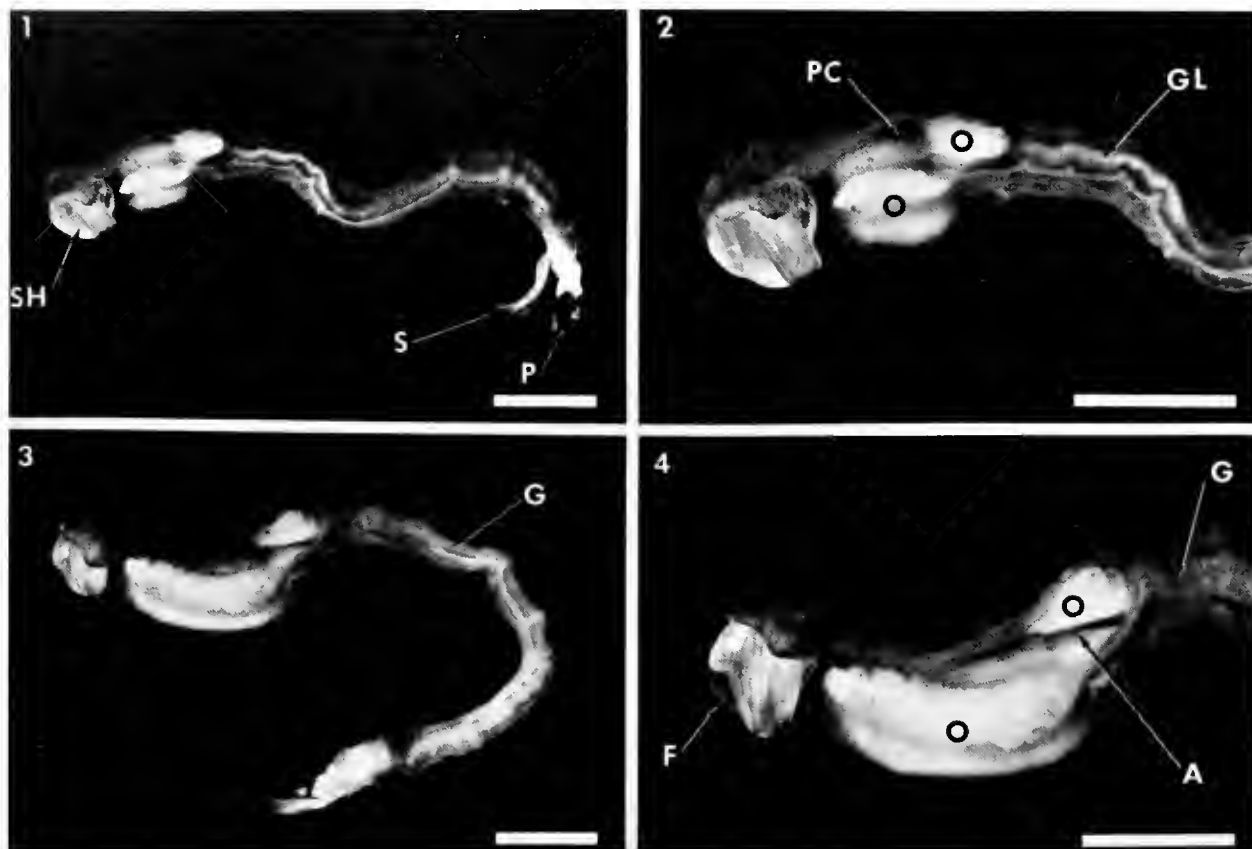
Figures 1 through 4. *Lyrodus floridanus.* Intact animal showing major anatomical features through the translucent mantle. (1) Left lateral view of an adult female that is brooding straight-hinge larvae in the gill. The enlarged ovaries indicate that it is in the latter stages of a gametogenic cycle (2.7✕). (2) Enlargement of anterior end of animal in Figure 1. Note straight-hinge larvae in gills and the enlarged ovaries (4.3✕). (3) Left lateral view of an adult female that has recently released larvae (gills are empty). The greatly enlarged ovaries indicate that spawning is imminent (2.7✕). (4) Enlargement of anterior end of animal in Figure 3 (4✕). Legend: A, auricle; F, foot; G, gill; GL, gill with larvae; O, ovary; P, pallets; PC, pericardium; S, siphon; SH, shell. Scale bar = 5 mm.

Immediately after spawning the lumina of the ovarian follicles and tubes are empty and appear as clear mantle-colored tissues arranged in a dendritic pattern on the surface of the caecum. The first observable change in the ovaries as gametogenesis proceeds is the appearance of oocytes in the lumina of the follicles. As the number of oocytes increases, the follicles enlarge, obscuring the dendritic pattern, and the ovaries begin to turn white (Figures 1 and 2). Just before spawning, greatly enlarged white ovaries completely cover the caecum laterally and dorsally and extend posterodorsally to terminate at the opening of the genital ducts (Figures 3 and 4).

Spawning is rapid, probably less than one hour in duration. At the conclusion of spawning the gonads are empty and clear. The eggs pass from the suprabranchial chamber into the water tubes of the gill, thereby turning the dorsal portion of the gills white. As development progresses the color of the gills change from white, when they contain eggs, embryos, or trochophore larvae, to pale lilac as the embryonic shell (prodissoconch I) forms, and then gradually to a bright lilac as the prodissoconch II begins to develop

and the larvae reach the straight-hinge stage. [The terms prodissoconch I and prodissoconch II are used in the sense of Waller (1981).] As the prodissoconch II begins forming, individual larval shells can be seen within the gill. Similar to spawning, larval release is rapid, probably requiring less than one hour. The larvae pass from the water tubes of the gill to the suprabranchial cavity and are expelled from the parent through the excurrent siphon. They develop to the settlement stage, competent pediveligers, as planktotrophic larvae.

One reproductive cycle, defined here as the time from one spawning to the next, is divisible into two parts that are readily observable by an examination of the gills. During the brood period, the time from spawning until larval release, the gills contain eggs, embroys, or larvae (Figures 1 and 2); during the empty period, the time from larval release until spawning, the gills are empty (Figures 3 and 4).

Observation of the animals continued until the female died on day 39. During this period, we observed four complete and two incomplete gametogenic cycles as well as five brood periods. The first gametogenic cycle was underway

when the animal was removed from the wood and the last cycle was in progress when the female died. Larvae from all five broods appeared normal. Straight-hinge larvae from brood 1 at the time of release measured 77.8 ± 1.4 μm long, 66.2 ± 1.6 μm high, and had a hinge length of 43.7 ± 0.3 μm (N = 20). These measurements agree closely with the size of larvae released from undisturbed animals living in wood (79.4 ± 4.2 μm long, 70.0 ± 1.4 μm high, and a hinge line of 47.4 ± 1.1 μm; N = 20). A small number of eggs was expelled from the parent at each spawning. Eggs in the germinal vesicle stage had a diameter of 52.0 ± 0.6 μm (N = 20) and approximated the size of the eggs of *Teredo navalis* (50 to 55 μm) reported by Culliney (1975). Throughout the remainder of the brood period very few larvae were released from the gills and these were usually associated with mechanical disturbance caused by changing the water and bowl.

Figure 5 is a diagrammatic representation of the gametogenic cycles and brood periods constructed from observations of the times of spawning and larval release. Times of spawning and larval release are designated as the midpoints between the times of successive observations (Figure 5). We recognize that Figure 5 is a qualified representation of the data. First, gametogenic cycles are considered to begin directly after spawning. This is not necessarily so. Although follicles appear empty at this time, gametogenesis could have already begun. Conversely, a period may exist between spawning and gametogenesis. Such a period would, however, be short because oocytes are seen in the ovarian follicles within one day after spawning. Second, the length of gametogenesis is unknown. Consequently, in Figure 5, gametogenic cycles are drawn as straight lines. The ovary fills gradually and empties rapidly. Third, the magnitudes of gametogenic cycles and brood periods are not quantified. They are represented simply as the condition of the gonads and gills. During our observations the size of the full gonads and gills did not differ perceptibly from gametogenic cycle to gametogenic cycle and from brood to brood. Therefore, magnitudes of both the gametogenic cycles and brood periods are diagrammed equally. It should be noted that the gills were empty during gametogenic cycle 1. The probable explanation for this is that, as so often happens when animals are removed from the water for long periods of time during transport to the laboratory, larvae are aborted
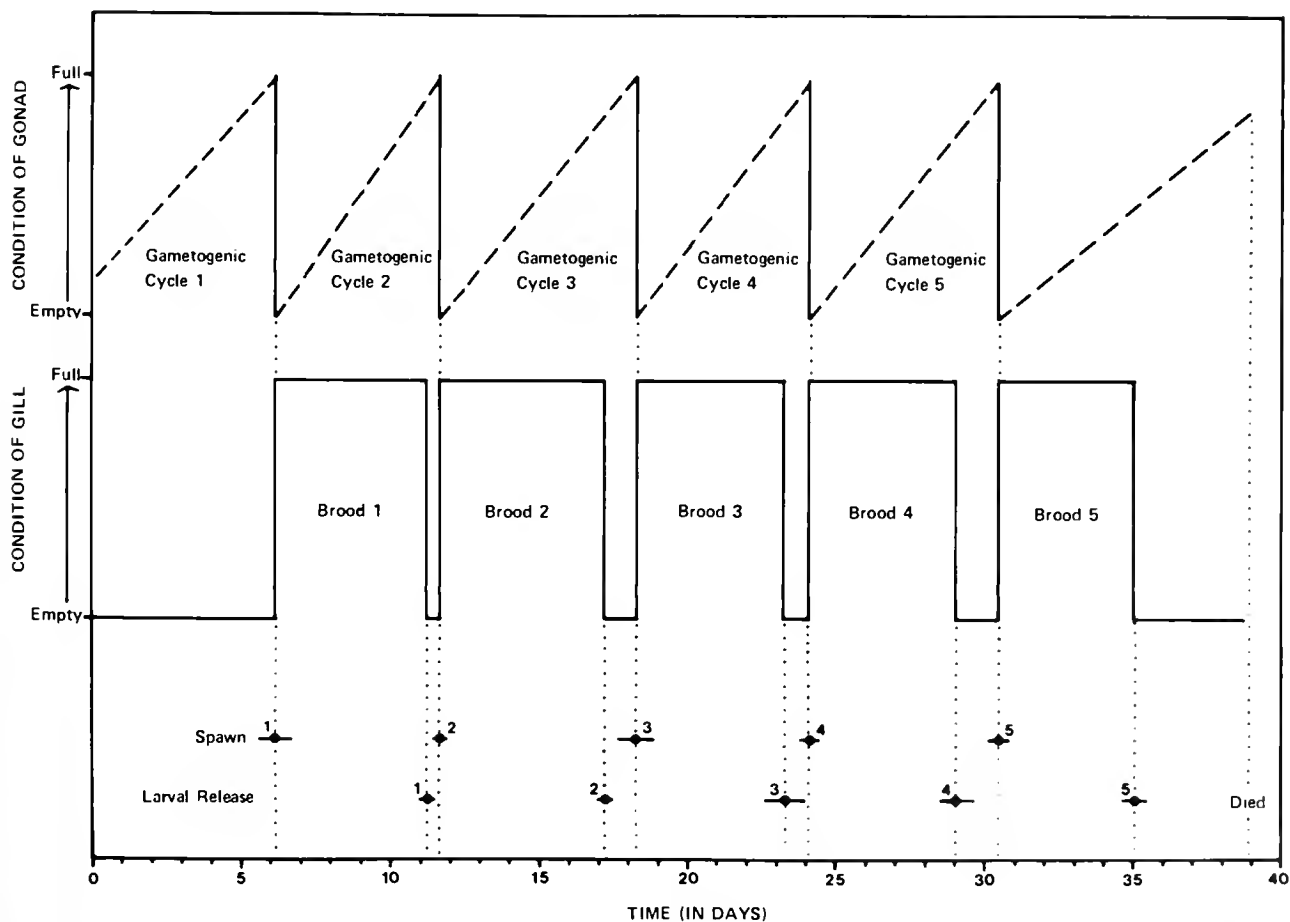
Figure 5. Diagrammatic representation of gametogenic cycles and brood periods constructed from the times of spawning and larval release observed in a single female *Lyrodus floridanus*. Spawning and larval release periods are figured as midpoints of successive observations.

at the time the panel is put into the aquarium. There were no larvae in the gills when the animal was dissected from the wood but gametogenic cycle 1 was underway. The greater length of this cycle possibly resulted from trauma induced by the collecting and dissecting procedures.

It is apparent from Figure 5 that: (1) gametogenic cycles are concurrent with brood periods so that the animals are ripe at the time of larval release and spawning of the next cohort occurs almost immediately, leaving only a short period when the gills are empty; and (2) durations of the gametogenic cycles and brood periods are regular, having mean times of 6.12 ± 0.49 days (N = 4) and 5.02 ± 0.38 days (N = 5), respectively. Our observations of the brood period of five days in *Lyrodus floridanus* maintained at 19 to 20°C are in close agreement with the report of a 5-day brood period in *Teredo navalis* grown at 25°C (Culliney 1975).

DISCUSSION

Breeding seasons of shipworms are largely based on field collections or panel studies because breeding seasons correspond roughly to dates of larval settlement (Scheltema and Truitt 1954, Nair and Saraswathy 1971). Characteristically, larvae settle throughout the year in most tropical marine areas and seasonally in high latitudes or areas of varying salinity. Three major life-history patterns are known for the Teredinidae: oviparous, short-term larviparous, and long-term larviparous (Turner 1966, 1971; Turner and Johnson 1971). We know the duration of the free-swimming larval period and relative fecundities per brood for these various life styles. Some estimates of numbers of eggs or larvae released during a given reproductive cycle have been published. For example, Sigerfoos (1908) estimated that a large female of *Teredo dilatata* Stimpson (= *Psiloteredo megotara* [Hanley]), an oviparous species, releases 10^8 eggs in a single spawning; Grave (1928) stated that a large specimen of *Teredo navalis*, a short-term brooder, produces 5 × 10^5 to 10^6 eggs per spawning; and Karande et al. (1968) reported that the brood of a 50-day old female of *Teredo furcifera* von Martens, a long-term brooder, contained $7 × 10^3$ larvae.

Two vital life-history statistics are missing for all of these species, i.e., the number and the size of broods and gametogenic cycles that occur during the life time of a given individual. Without these data we cannot determine total fecundity of an individual nor can we meaningfully compare fecundities of species with different reproductive patterns. The most direct way to obtain these data is to observe single animals; however, in the Teredinidae this type of study is not without problems. To observe individual shipworms, we removed them from the wood and could feed them only on phytoplankton. The animals were undoubtedly stressed, but, nevertheless, the durations of the gametogenic cycles and brood periods were typical of those for *Teredo navalis* and probably for other short-term

larviparous species. If one could have only a single animal per panel and could pair a male and a female in the same aquarium the problem of stress would largely be eliminated. It would then be possible to observe times of spawning in oviparous species or larval release in larviparous species. Unfortunately, in the case of larviparous species, only the number of broods and the length of the reproductive cycle could be determined because spawning could not be observed. It is, of course, impossible to obtain data from the same animal on both the total number of eggs or larvae produced and the time course of gametogenesis, because the latter would require histological examination. However, the magnitude of each brood can be determined by counting eggs spawned or larvae released. In larviparous species, if it is assumed that no wholesale disintegration of eggs or embryos occurs in the gills (we have seen no evidence of this), then the number of eggs produced per gametogenic cycle can be determined indirectly as the sum of aborted embryos, aborted larvae, and released larvae.

Crisp and Davies (1955) have shown that if the values of reproductive cycles and brood periods do not vary widely about their means, then the fraction of the population which is brooding is equal to the mean brood period divided by the mean reproductive period. If the durations of the brood and reproductive periods recorded for the single *Lyrodus floridanus* which we observed are representative of the population of *L. floridanus* in our test panels, then 87% of these animals would be brooding at a given time. During the breeding season (which in Florida extends at least from February through September and is probably year around), we have often noted that the vast majority of specimens dissected from the test panels were indeed brooding.

This study, which began as a fortuitous observation, dramatically illustrates another large gap in our knowledge of the reproductive biology of the Teredinidae. A survey of the marine invertebrate literature indicates that studies of the reproduction of single animals with time are rare. The paper on breeding of the barnacle *Elminius modestus*, by Crisp and Davies (1955), is an excellent example of how such investigations might be designed.

CONCLUSIONS

The documented rapid successive broods and gametogenic cycles in *Lyrodus floridanus* were unexpected and explain why a large percentage of the animals in our collecting panels contained eggs and larvae. These brood periods and gametogenic cycles may also explain the population explosions of short-term larviparous species that, when introduced into a new area, may surpass native oviparous species.

Turner (1966) considered *L. floridanus* a synonym of *L. pedicellatus* mainly on the basis of shells and pallets of preserved specimens. After observing living specimens in Puerto Rico, Turner and Johnson (1971) suggested that

the *pedicellatus*-like *Lyrodus*, which released large numbers of straight-hinge larvae, might be another species. Results of the present research, combined with our unpublished observations on morphological differences of the brood pouches and of larvae, confirm the earlier suspicions of Turner and Johnson (1971) that *L. floridanus* and *L. pedicellatus* are distinct species. The former broods its larvae only to the straight-hinge stage and then releases them en masse; the latter broods to the pediveliger stage, carries several cohorts of larvae at different stages of development, and releases only a few young at a time. Unfortunately, young and nonbreeding specimens of these two species are difficulty, if not impossible, to distinguish.

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RESEARCH NOTE

SETTLEMENT OF SPAT OF THE PURPLE–HINGE ROCK SCALLOP *HINNITES MULTIRUGOSUS* (GALE) ON ARTIFICIAL COLLECTORS

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ABSTRACT   Various artificial collectors were tested to obtain spat of the purple-hinge rock scallop *Hinnites multirugosus* (Gale). These included plastic-mesh onion bags which were filled with nylon monofilament (gillnet), monofilament dipped in cement, chaparral sticks, and a combination of sticks and empty scallop shells. The collectors were placed near a rock scallop population in Mission Bay, San Diego, CA. The length of exposure and spatfall by season were also investigated. Spat recruitment was greatest in gillnet collectors immersed for 3 to 4 months between late March and July. Up to 47 spat of *H. multirugosus* (7 to 12 mm L) per gillnet bag were caught. Numerous spat of the blue mussel *Mytilus edulis* Linné and the wide-eared scallop *Leptopecten latiauratus* (Conrad) also settled in the gillnet collectors.

KEY WORDS: Rock scallop, *Hinnites*, spat collectors, spatfall, spat recruitment, aquaculture, mariculture.

INTRODUCTION

The purple-hinge rock scallop *Hinnites multirugosus* (Gale) ranges from central Baja California to southern Alaska and is common from the low-tide mark to 55 m (Abbott 1974). Unlike the Atlantic bay scallop *Argopecten irradians* (Lamarck) and the Atlantic deep-sea scallop *Placopecten magellanicus* (Gmelin), which are free-swimming as adults, *H. multirugosus* cements itself to firm substrate after a 6-month, free-swimming, juvenile (spat) stage. Like the bay scallop it may temporarily attach by byssal threads. The sessile nature of the adult has promoted considerable aquaculture research with this species (Leighton and Phleger, 1976, 1977, 1981; Cary et al. 1981). During this study we addressed the problem of obtaining spat in sufficient numbers for research or aquaculture development and we employed experimental spat collectors to determine the best settlement substrate, the appropriate immersion time, and the period of greatest spatfall.

Spat of the Japanese scallop *Patinopecten yessoensis* (Jay) can be collected with 1-mm mesh bags that contained monofilament gillnetting (Ito et al. 1975). Spat of *P. magellanicus* have been collected in 1.5-mm mesh onion bags which were filled with monofilament gillnetting (Naidu et al. 1981). Spat of the common European scallop *Pecten maximus* (Linné) have been collected with Netlon® mesh envelopes which contained nylon and plastic meshes and teased polypropylene rope (Brand et al. 1980). Thin monofilament nylon has also been used as a substrate for settlement of spat of the Iceland scallop *Chlamys islandica* (Müller) (Wallace 1981/82).

The molluscan taxonomy follows that of Abbott (1974) for all but a few of the common bivalve names.

MATERIALS AND METHODS

Two principle types of spat collectors were used in this study: (1) onion bags that contained 600 to 900 g of loose, aquamarine monofilament (twine size #14, gillnetting), and (2) plastic screen bags that were filled with dry chaparral sticks. All of the bags were 42 × 75 cm and 1.0 to 1.5-mm mesh size. Spat bags were tied to concrete pier pilings at a depth of 3 to 4 m and 3 m above the bottom on the Ventura Bridge, Mission Bay, San Diego, CA, among a large population of purple-hinge rock scallops. All deployment and retrieval of the spat bags were accomplished by skin divers.

Scallops often attach to cement pilings. A series of spat bags which contained gillnetting were partially coated with Redi-Crete® cement to test its effectiveness as an attractant. The cement dried and adhered readily to the monofilament strands. Old rock scallop shells were included in a group of screen bags (20 shells per bag) which also contained chaparral sticks to act as an inducement for settling scallop spat.

Spat collectors were placed in the bay during the two rock scallop spawning periods, late spring and late fall (Jacobsen 1977). Fourteen gillnet bags (seven dipped in cement) were placed in Mission Bay during December 1981, and retrieved in March 1982. Twelve gillnet bags (without cement) were placed in the same location and at the same depth during March and June 1981. To determine the time of spat settlement and seasonal growth rate, three bags were retrieved at monthly intervals from June to September 1981. Screen spat bags with chaparral sticks were placed in the same Mission Bay location as the gillnet bags during spring 1981. Eight stick-filled bags were placed in the bay during April, May, and June 1981, and retrieved at 3-month

intervals. After retrieval, the spat bags were transferred to a dock in Mission Bay and all newly settled scallops were removed and counted. Because numerous invertebrates attached to the gillnetting in addition to the rock scallops, the gillnetting was repeatedly washed and shaken in sea water in shallow plastic tubs to separate and recover the spat and associated organisms.

RESULTS AND DISCUSSION

The spat of *H. multirugosus* were most abundant on the gillnet collectors. Up to 47 spat occurred per bag and ranged in length from 2 to 12 mm (mean lengths = 4 to 7 mm). Plastic screen bags of sticks were much less effective in attracting the spat. The total numbers of spat in the stick-filled bags ranged from 0 to 6, and spat lengths ranged from 3 to 9 mm (mean lengths = 5 to 7 mm). All 26 of the gillnet spat collectors contained rock scallop spat, while only 6 of the 24 stick-filled collectors from the same location contained rock scallop spat. A Student's *T*-test showed no significant difference at the p = 0.01 level between *H. multirugosus* recruitment on cement-dipped gillnetting and undipped gillnetting (Table 1). The addition of old scallop shells to the stick-filled bags did not increase recruitment. No rock scallop spat settled in two sets of four stick-filled bags with and without old scallop shells which were set in the bay at the same time and location. The success of gillnetting versus other substrates may reflect its larger area for attachment and subsequent growth of the scallop larvae and spat.

Spat of the wide-eared (bay) scallop *Leptopecten latiauratus* (Conrad) were invariably present in numbers of up to 437 in gillnet collectors and up to 206 in stick-filled collectors. Approximately 50% of the spat of *L. latiauratus* were dead (single shells or fragments), whereas all of the spat of *H. multirugosus* were alive in the overwintered gillnet collectors. Two bags with low numbers of spat (bags 2 and 3, without cement, Table 1) were torn open and contained entangled fish hooks. Up to 100 living crabs (*Cancer* spp.) were observed in the torn bags.

The time of spat settlement is important in the deployment of collectors for rock scallop spat. More spat attached during the spring and early summer than during the preceding winter at the same location in Mission Bay. The numbers of spat of *H. multirugosus* per bag ranged from 14 to 43 during three months in spring (24 March to 24 June 1982). The numbers of spat collected during the preceding winter (Decmeber 1981 to March 1982) ranged from 2 to 24 (Table 1). In our previous study of recruitment of rock scallops on the undersides of rock jetties in Mission Bay during 1976 and 1977 (Leighton and Phleger 1981), we also found small juveniles (3 to 10 mm, length) to be abundant during late spring and early summer. Spatfall data from the stick-filled bags showed that recruitment ceased during May 1982. Eight stick-filled bags which were deployed on 24 April 1982 and recovered on 24 June 1982 contained 16 spat (mean length = 6 mm). Spat length data suggest that recruitment occurred only in March and April because 2-mm spat were about 2 months post-settlement. Spring (March to April), therefore, appears to be the most appropriate time for deploying spat collectors for *H. multirugosus* in southern California.

The fact that spat collectors, which were deployed during spring and early summer, also contained large numbers of spat of the blue mussel *Mytilus edulis* Linné (2,000 to 10,000 per bag) suggests that the rock scallop spatset may have been much greater if there had not been such apparent competition for setting space. Spat collectors that contained gillnetting and that were over-wintered in the bay contained only a few hundred blue mussel spat each. Other invertebrates which were recovered from the spat collectors included free-living flatworms, juvenile gastropods, Hemphil's swimming scallop *Lima hemphilli* Hertlein and Strong, juveniles of *Chione* sp., pholad clams, polychaete scale and serpulid worms, brachyuran crabs including *Cancer* sp.,

TABLE 1.

Results of trials with dipped and undipped spat collectors deployed in Mission Bay, San Diego, California
between December 1981 and March 1982.

	Cement-Dipped Monofilament Gillnetting				Monofilament Gillnetting Without Cement		
Bag No.	*Leptopecten latiauratus*	*Hinnites multirugosus*	Percent of Total (*H. multirugosus*)	Bag No.	*Leptopecten latiauratus*	*Hinnites multirugosus*	Percent of Total (*H. multirugosus*)
1	134	10	7.5	1	115	5	4.3
2	151	16	10.6	2	32	4	12.5
3	172	24	14.0	3	9	4	44.4
4	113	4	3.5	4	164	6	3.7
5	114	2	1.8	5	175	10	5.7
6	90	3	3.3	6	92	6	6.5
7	206	6	2.9	7	86	14	16.3
Totals	980	65	6.6	Totals	673	49	7.3
Means	140	9		Means	96	7	

isopods, amphipods, arborescent bryozoans, juveniles of the seastars *Pisaster* spp. and *Asterina miniata* (Brandt), and the tunicate *Ciona intestinalis* (Linné). A few fish in the genera *Hyposoblennius* and *Girella* were also recovered from the spat collectors.

Spat collectors should not be deployed in the bay for more than 4 months at a time. After 6 to 7 months of immersion, numerous spat of *H. multirugosus* and almost all spat of *L. latiauratus* were dead; we recovered mostly single, empty, and many fragmented shells. The definitive causes of spat mortality are unknown. Possible causes include (1) anoxia detected in the spat collectors (H_2S odor and black sediment) which were held for 5 to 6 months, and (2) crab (*Cancer* sp. and another unknown species) and seastar (*Pisaster* spp.) predation. In some cases 25 to 100 crabs were recovered from infested spat collectors. We do not know why anoxia and crab predation did not occur prior to 5 or 6 months of exposure. The shells of *L. latiauratus* appear to be thinner than those of *H. multirugosus* and, therefore, more susceptible to crab predation. Spat collectors that were deployed for 3 to 4 months contained live spat of *H. multirugosus,* but only empty or fragmented shells of *L. latiauratus.*

This study indicated that spat collectors may represent a practical method of obtaining large numbers of juveniles (spat) of the purple-hinge rock scallop for an aquaculture industry. Seasonability and total immersion time appear to be the major factors that control the deployment and effectiveness of spat collectors for *H. multirugosus.*

ACKNOWLEDGMENTS

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ABSTRACTS OF TECHNICAL PAPERS

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A STUDY OF BLUE CRAB POPULATIONS IN CHESAPEAKE BAY IN THE VICINITY OF THE CALVERT CLIFFS NUCLEAR POWER PLANT, 1968–1982

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Blue crab (*Callinectes sapidus*) population data were collected from 1968 to 1981 to determine the effects of waste heat from the Calvert Cliffs Nuclear Power Plant (CCNPP) on abundance, size distribution, sex ratios, and seasonality. Crabs were sampled using commercial crab pots of 2.5-cm mesh set within (Plant Site) and outside (Kenwood Beach and Rocky Point) the main thermal-effect area. Five pots per station were fished 4 days/week during alternate weeks from May through November. Crabs were sexed, measured, and weighed by sex. In 14 years, a total of 10,552 pots yielded 57,144 crabs (5.42/pot) of which 74.1% were legal size ($\geq$ 127 mm carapace width) and 51.6% were male. During 7 preoperational years (1968–74), crabs/pot averaged 4.06 at Kenwood Beach (33.3%), 3.94 at Plant Site (32.3%), and 4.18 at Rocky Point (34.3%). During 7 operational years (1975–81), crabs/pot averaged 6.24 at Kenwood Beach (33.3%), 6.37 at Plant Site (34.0%), and 6.13 at Rocky Point (32.7%). Increased catch during the operational period was due to extreme abundance in 1981 when pots averaged nearly 17 crabs. Data analyses revealed no significant station differences other than a higher percentage of males at Kenwood Beach than at Rocky Point (p=0.005). There has also been a significant decrease in percent males since 1968 (p < 0.001) which has occurred equally at all stations. No effect of the CCNPP on crab populations was evident from these studies.

REPRODUCTION AND DEVELOPMENT IN THE LUCINID CLAM *CODAKIA ORBICULARIS* LINNÉ

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The tiger lucine *Codakia orbicularis* is a large edible clam currently being investigated as a mariculture candidate in the Bahamas Islands. Gonad development and spawning seasons were assessed by monthly sampling of *C. orbicularis* from Grand Bahama Island and Key Biscayne, Florida. Histological examination of clams exceeding 20 mm in shell length showed most of the populations sampled ripe between April and November. Natural spawning probably occurs from May to October.

Clams seldom respond to standard spawning techniques, including physical and chemical stimuli. Artificial fertilization by carefully stripping the gonads produced 15 to 20% viable embryos. Eggs are 108 to 112 μm in diameter and are encased in a thick capsular membrane. Following fertilization, the gastrula, trochophore, and early veliger stages develop within the capsular membrane. Upon hatching, the planktonic veliger ranges from 150 to 174 μm in shell length and develops to the pediveliger stage in approximately 12 days. Metamorphosis occurs approximately 16 days after fertilization. Larval growth and developmental features peculiar to *C. orbicularis* are discussed.

EFFECTS OF INORGANIC PARTICLES ON THE GROWTH OF THE EASTERN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN)

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The effect of seven concentrations of inorganic particles (oxidized silt from the Broadkill River) on the growth of oysters (*Crassostrea virginica*) was studied at each of three algal ration levels. In the absence of silt (zero concentration) oyster growth was not significantly different between the selected algal ration levels. At the lowest algal ration, the addition of silt did not significantly affect oyster growth rate; however, at the medium and high algal ration levels oyster growth did increase with increasing silt concentration up to 25 mg/ℓ. Above 25 mg/ℓ, up to 150 mg/ℓ, the increased growth rate level was maintained showing neither further enhancement nor any adverse effect on oyster growth. The silt effect is discussed in terms of improved delivery of food, growth factors, toxic metabolites, increased digestability, resuspension of pseudofaeces, and increased filtration and ingestion rates. Implications of the findings for bivalve molluscan mariculture are suggested. The increased growth rate could not be explained by any single mechanism.

APPLICATIONS OF FLOW CYTOMETRY TO CYTOGENETIC STUDIES IN BIVALVE MOLLUSCS: MEASURING CHANGES IN DNA CONTENT

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Flow cytometry is a relatively new approach to cytogenetic studies in the biomedical field. This technique is of considerable utility in other fields, especially in measuring quantum shifts in DNA content. Diploid and triploid oysters and clams were subjected to tissue disaggregation and nuclei isolation techniques in an attempt to derive a suspended cell population for analysis. Tissue disaggregation was shown to be most effective and the principles of this method are described. Nonlethal analysis of DNA content in individual bivalves was also accomplished by sampling cells from hemolymph sinuses. An apparent quantum duplication of DNA between the sea scallop and bay scallop was demonstrated. Recommendations for continued investigations using flow cytometry are presented.

OBSERVATIONS ON THE GROWTH AND SURVIVAL OF LABORATORY-REARED JUVENILE CONCHS, *STROMBUS GIGAS* AND *S. COSTATUS*

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A study of the culture and life history of the queen conch *Strombus gigas* Linné in Puerto Rico has been underway since 1981. Its objective is to develop suitable methods for the large-scale culture of larvae of *S. gigas* and subsequent release of juveniles to rebuild depleted natural stocks. Although efforts have concentrated on *S. gigas*, larvae of the closely related milk conch *S. costatus* Gmelin have also been raised. Larvae were raised from eggs collected from the field. The larval period was variable with settlement commencing from 12 to 19 ($\bar{x}$ = 15.6) days after hatching. Length at metamorphosis varied from 1.2 to 1.8 mm with a mode between 1.4 and 1.5 mm. Sets of over 1,000 juveniles were achieved with survival ranging from 4 to 7% from hatching to a postmetamorphosis size of 3 to 5 mm. After metamorphosis growth increased noticeably. Initial postmetamorphosis growth was 0.2 mm/day, but the rate of growth continued to increase reaching a mean of 4 mm/day through the first 200 days. Feeding experiments of juveniles indicated that the macroalga *Spyridia filamentosa* (Wulfen) was preferred.

Pilot experiments involving the release of small (25 to 50 mm) tagged juveniles permitted the testing of suitable mark and recapture methods and the collection of preliminary observations of juvenile behavior. These observations indicated that mortality was initially high but dropped over time. Dispersal has been slow and random. Observed growth was slow, probably caused by the large amount of time spent buried and hence inactive.

A SIMULATION STUDY OF A STOCHASTIC MODEL FOR *MYA ARENARIA*

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Field data presented by Brousseau (1978, 1979) provided estimates of age-specific fecundity and survival for the softshell clam *Mya arenaria*. We have used these values in a Leslie population model (1945, 1948) to estimate an equilibrium settlement rate for clams in the first age class (Brousseau et al., in press). Settlement rates are highly variable in nature, however, and the modelling efforts incorporate this phenomenon. An optimal harvesting strategy based upon the Leslie model was published by Rorres and Fair (1975). We have designed simulation studies which adapt their procedure as well as other similar procedures to a stochastic environment and applied these strategies using the *Mya* model. Preliminary results show that these methods do not over exploit the population; however, they may be too conservative.

AN EXPERIMENTAL HABITAT POT FOR PREMOLT CRAB CAPTURE

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Three years of testing premolt (peeler) crab capturing devices showed unbaited habitat pots to be a potential harvest gear in South Carolina estuaries. Two and one-half-centimeter mesh wire was used for pot construction, and pot design was similar to that for baited hard crab pots. Tests were conducted 4 consecutive days/week in the Ashley

River from mid-April through mid-November, 1979, and daily in the Wando River from April through June, 1980 and 1981. Primary objectives were to increase pot efficacy and reduce pot construction cost and labor.

Results showed that plastic flagging tape interwoven among the wire mesh did not increase catch rates: pots with and without tape averaged 0.7 peeler/gear-day (one pot with a soak time of 24 h). Two large entrance pots (61 × 61 × 45 cm) outfished 4 small entrance pots (61 × 61 × 30 cm) by 1.6 vs. 1.3 peelers/gear-day, respectively. Pots fished in shallow subtidal mudflats captured a mean of 1.7 peelers/gear-day whereas those in deep water (> 3 m) captured only 0.7 peeler/gear-day. Highest capture rates were obtained in June during each year. A maximum of 3.5 peelers/gear-day was obtained when large habitat pots were fished on shallow water mudflats in June. Male peelers accounted for 63% of 1,832 peelers caught in habitat pots during 1981. Habitat pots require no bait and offer crabbers a method of harvesting peelers in relatively consistent numbers throughout the shedding season.

REFUGES FROM BLUE CRAB (*CALLINECTES SAPIDUS* RATHBUN) PREDATION FOR INFAUNAL BIVALVES IN THE CHESAPEAKE BAY

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Direct measurements of valve strength of various sizes of *Mya arenaria* Linné, *Macoma balthica* (Linné), *Macoma mitchelli* Dall, and *Mulinia lateralis* (Say) compared to measurements of blue crab chelae grip strength suggest that the shells of these infaunal bivalves confer no resistance to crushing by blue crabs. Also, blue crabs readily crushed these species in the laboratory.

Possible refuges from predation afforded to these infaunal bivalves were investigated. Bivalve size, depth of burrowing, and density were measured in the field throughout spring and summer 1981. This survey, in conjunction with laboratory feeding experiments that offered *M. arenaria* burrowed at various sediment depths to blue crabs, suggested that *M. arenaria* and *M. balthica* obtain refuge from blue crab predation at deeper sediment depths. Bivalves burrowed beneath an artificial submerged aquatic vegetation structure also gained additional protection. These refuges, however, were not absolute, but only relative to infauna burrowed less deeply or in bare sand (mud) environments. Yearly sampling

of bivalve infauna in the Choptank River, Chesapeake Bay, suggested that *M. mitchelli* and *M. lateralis* are able to persist despite predation due to their high reproductive output.

A RANDOM SAMPLE SURVEY TO ESTIMATE BLUE CRAB CATCH IN MARYLAND

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In June 1981 the Maryland Department of Natural Resources (MDNR) began operating a new system to estimate the catch of blue crabs (*Callinectes sapidus* Rathbun) in Maryland waters. The basis of the system is a stratified, random sampling design developed by the Martin Marietta Corporation, which allows MDNR to reliably estimate total crab catch in Maryland by asking only a small fraction of all crabbers to report their catch each month. This method produced a total annual harvest estimate in 1981 of 29.5 × 10⁶ kg (65 × 10⁶ lb) live weight, nearly twice the highest estimate produced under past systems. The estimate is based on standard statistical techniques, and takes into account the previously ignored factors of non-reporting by some crabbers and the non-commercial catch. Estimates of fisherman effort are produced concurrently.

WHAT DETERMINES THE VULNERABILITY OF BIVALVE PREY TO HORSESHOE CRAB PREDATION?

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Adult horseshoe crabs, *Limulus polyphemus* (L.), were offered combinations of different size and species of bivalve prey in a large aquarium. *Gemma gemma* (Totten) (Veneridae), a small, thick shelled species, was avoided when larger, thinner shelled clams such as *Mulinia lateralis* (Say) (Mactridae) or *Mya arenaria* Linné (Myidae) were available. Crabs did not differentiate between *M. lateralis* and *M. arenaria* of comparable size; however, there was a preference for *M. lateralis* over hard-shell clams, *Mercenaria mercenaria* (Linné) (Veneridae), of equal size. Large individuals of *M. lateralis*, > 10-mm shell length, were preferred over smaller individuals of *M. lateralis*. Thus, both shell length and shell thickness appear to influence the preference of horseshoe crabs for bivalve prey. The largest available prey species offered to *L. polyphemus* was *Spisula solidissima*

(Dillwyn) (Mactridae); clams up to 45-mm shell length were successfully opened. The method of consuming these bivalves differed from the manner in which smaller prey were handled, and is illustrated.

CLAM PREDATION BY SCOTER DUCKS IN THE STRAIT OF GEORGIA, BRITISH COLUMBIA

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Collections of three species of wintering scoter ducks, the white-winged scoter, *Melanitta deglandi* (Bonaparte), the surf scoter, *M. perspicillata* (Linnaeus), and the black scoter, *Oidemia nigra* (Linnaeus), were made at two clam beaches in southern British Columbia. Analyses of the crop and gizzard contents showed that these ducks were feeding primarily in the intertidal beach area. Molluscs, particularly bivalves, were the most important food items in the diet. The commercially important littleneck and Manila clams, *Protothaca staminea* (Conrad) and *Tapes philippinarum* (Adams and Reeve), respectively,comprised about two thirds of the gut contents of the scoters. Scoters are important clam predators in southern British Columbia; it was estimated that a wintering flock of 200 scoters could remove 5 to 14.5 metric tons of littleneck and/or Manila clams from these two beaches in a 6-mo period.

DETERMINATION OF SETTLEMENT RATES IN SHELLFISH POPULATIONS USING *MYA ARENARIA* LINNÉ AS A MODEL

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Egg loss, larval recruitment, and early post-larval mortality are often limiting factors in the establishment and maintenance of shellfish stocks; therefore, it is of interest to ecologists to be able to make estimates of settlement rates in such populations. This paper describes an indirect method for estimating mortality rates during settlement in shellfish populations for which demographic parameters (age-specific fecundity and survivorship) are available. The equilibrium settlement rate for a population of *Mya arenaria* from Gloucester, MA, was calculated using the Leslie matrix. Empirically derived demographic parameters indicate that the theroretical settlement rate required to maintain a steady state population is 0.001462% or one egg out of approximately 68,400 surviving to a size of 2 mm.

HEAVY METAL BINDING TO PROTEINS OF THE BLUE CRAB *CALLINECTES SAPIDUS* RATHBUN

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Hemocyanin is the large, extracellular oxygen transporting protein found in the hemolymph of the blue crab. The oxygen-binding site consists of a binuclear copper center. In addition to copper, blue crab hemocyanin invariably contains a small amount of tightly bound zinc (approximately 0.2 atom of zinc per oxygen-binding site). This observation, together with the fact that hemocyanins act at the interface between the organism and its environment, prompted us to investigate a possible role of these respiratory proteins in trace metal transport or toxicity in the blue crab. *In vitro* studies revealed that blue crab hemocyanin can indeed bind a variety of heavy metal ions, all with very high affinities (18 mercury, 14 cadmium, and 24 zinc ions per oxygen-binding site). The interaction of cadmium and zinc ions with blue crab hemocyanin increases its oxygen affinity; mercuric ions have an opposite effect. All three heavy metal ions reduce the degree of cooperativity in oxygen binding. Cadmium and zinc ions were found to substitute for calcium, which is a natural modulator of blue crab hemocyanin function.

In vivo exposure of blue crabs to cadmium dissolved in a flowing seawater system at 0.1 ppm or to cadmium-ladened oysters did not result in measurable elevated levels of cadmium in the hemolymph. The sites of cadmium accumulation varied depending on the method of exposure. Seawater-exposed crabs accumulated most of the cadmium in the gills; the ions were bound to a low molecular-weight protein (MW ~ 10,000). This protein was purified by gel-permeation chromatography and ion-exchange chromatography. Cadmium was the only metal associated with the purified protein. Crabs exposed to cadmium-ladened oysters accumulated most of the cadmium in the hepatopancreas, where it was associated with a low molecular-weight cadmium/zinc-binding protein. Ion-exchange chromatography showed the gill and hepatopancreas proteins to be different, suggesting that these proteins, which are presumably involved in trace metal detoxification, are tissue specific.

THE ROLE OF CARBON FILTRATION IN CULTURING THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA*

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Embryos and larvae of the American oyster *Crassostrea virginica* (Gmelin) were reared in two types of "disinfected" seawater. One type was filtered through two 10-μm orlon filters and UV-irradiated; the second type was subjected to the same treatments, except that an additional filtration process through a carbon cartridge was inserted prior to the UV irradiation step. The study compared embryonic development of the 2-day-old larval stage, as well as survival and growth of larvae to metamorphosis in the two types of treated seawater. Data indicated that the percentage of live-normal development was significantly greater in seawater subjected to carbon filtration than in seawater without this added treatment. Other data suggested success in rearing oyster larvae to metamorphosis using carbon filtration only when the larval cultures were changed daily. Seawater treatment is but one aspect of the prevention regimen to be followed. Sound sanitary practices also are described to reduce the frequency of disease outbreaks in hatcheries.

MOVING OUT THE LEARNING CURVE: AN ANALYSIS OF NURSERY OPERATIONS FOR THE HARD CLAM *MERCENARIA MERCENARIA* (LINNÉ) IN SOUTH CAROLINA

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Trident Seafarms (a private corporation) and the State of South Carolina (SC Wildlife and Marine Resources Department) entered into a cooperative research agreement for the commercial production of hard clams in 1980. The SC Sea Grant Consortium provided partial funding for the scientific research and some staff time for the economic analysis of the first 15 months of nursery operation. Detailed cost and production analysis are provided, along with a description of the evolution of the nursery production protocols and of the nursery design. During the period from September 1980 to December 1981, 19,733,000 seed clams were imported into the nursery; of these 13,008,000 remained in the nursery at the end of the year, 3,402,000 were planted in the field with 14,700 returned to the nursery. The apparent mortality was 3,337,700 clams during the 15 months. This 16.9% mortality is misleading because of the rapidly increasing number of clams in the nursery over the period of the analysis. Beginning with the correction for mortality, a detailed budget analysis is given and linear programming is employed to determine optimal importation strategies.

A SURVEY OF ALLOZYME VARIATION AND ESTIMATES OF GENETIC SIMILARITY AMONG THREE *OSTREA* SPECIES

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Three nonsibling *Ostrea* species (i.e., *O. edulis* Linné, *O. lurida* Carpenter, and *O. permollis* Sowerby) were studied by horizontal protein electrophoresis with relation to levels of genetic variation and similarity. The percentages of polymorphic loci per species were estimated as 27.6, 37.0, and 52.0 for *O. edulis*, *O. lurida*, and *O. permollis*, respectively, based on an examination of 25 to 29 structural loci. The mean observed heterozygosities per individual were estimated as 9, 16, and 15% for *O. edulis*, *O. lurida*, and *O. permollis*, respectively. A pairwise comparison of loci was made between species which indicated that approximately 17% of the loci studies were genetically identical while 55% had no genetic similarity. The mean genetic identity across all loci among the three species was estimated as 24.5%. Finally, there seemed to be a correlation between the dispersal time of the planktonic larvae and the levels of genetic variation found within these nonsibling *Ostrea* species.

THE SOUTHERN OYSTER DRILL: A PREDATOR OF TRAPPED BLUE CRABS

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Southern oyster drills (*Thais haemastoma floridana* [Conrad]) are reported for the first time to attack and kill mature blue crabs (*Callinectes sapidus* Rathbun) in commercial crab pots. Trapped blue crabs were attacked by as many as 54 drills of up to 80 mm in shell height. All affected crabs were either ovigerous or recently spent females, and all were simultaneously infested with the symbiotic acorn

barnacle *Chelonibia patula* (Ranzani). Entry portals for the proboscis of feeding drills included: (1) open skeletal wounds caused by other trapped crabs, (2) internal skeletal openings between the branchial chamber and the infrabranchial sinuses at the bases of the gills, (3) stumps of autotomized pereiopods, and (4) holes rasped in the exoskeleton by the snails' radulae. The attacks were attributed to at least two factors: the presence of large numbers of drills in the crab harvest area in the vicinity of Mississippi's offshore barrier islands, and the opportunistic feeding behavior of the drills, especially when confined with trapped crabs. Moribund and/or dead crabs also attracted another carnivorous snail, the cancellate cantharus, *Cantharus cancellarius* (Conrad).

FACTORS AFFECTING DOCKSIDE PRICES FOR HARD BLUE CRABS IN CHESAPEAKE BAY

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The nature and the magnitude of selected factors hypothesized to influence the ex-vessel price of hard blue crabs in Chesapeake Bay were investigated. The data base used consisted of monthly observations for the period January 1973 to June 1980. Seasonality, landings of hard blue crabs in Chesapeake Bay, and the wholesale price of hard blue crabs had significant impacts on the ex-vessel price. Landings of hard blue crabs in the south Atlantic and the Gulf were not statistically significant in influencing the ex-vessel price of hard blue crabs in Chesapeake Bay. On the basis of the estimated flexibility coefficients, total revenue to harvesters could be incremented by increasing landings in Chesapeake Bay throughout each season of the year.

MOLLUSCAN SHELL DISSOLUTION BY PENETRATING EUMETAZOAN INVERTEBRATES: AN HYPOTHESIS ON THE CHEMICAL MECHANISM BASED ON ULTRASTRUCTURE

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Of the 27 eumetazoan invertebrate phyla generally recognized, at least 8 widely separated ones are known to contain shell penetrating species (burrowers or borers): Platyhelminthes, Bryozoa, Sipunculoidea, Phoronida, Annelida, Arthropoda, Brachiopoda, and Mollusca. The pattern of molluscan shell dissolution is similar at the ultrastructural level in species of four phyla that have been studied:

polychaete *Polydora websteri* Hartman (Zottoli and Carriker 1974), barnacle *Trypetesa lampas* (Hancock) (Todd 1981), gastropod *Urosalpinx cinerea* (SayY) (Carriker 1978), and cephalopod *Octopus vulgaris* Cuvier (Nixon et al. 1980). A secretion weakens the shell surface by initially solubilizing the nonmineralized intercrystalline organic matrix between individual mineral cores of shell units, then dissolves exposed mineral cores; dissolution of organic matrix and mineral cores then proceeds at more or less equal rates, solubilization of the organic matrix ahead of mineral cores, the latter frequently irregular and pitted. The secretion of the accessory boring organ of *U. cinerea*, hypothesized to contain a combination possibly of HC1, chelating agent, and enzyme (Carriker 1981) could produce the differential dissolution observed ultrastructurally. Similarity of the pattern of etching produced in shell penetration of *P. websteri*, *T. lampas*, *U. cinerea*, and *O. vulgaris* suggests the existence of a generically similar chemical mechanism in the shell-penetrating Eumatozoa.

COMPOSTING OF BLUE CRAB SCRAP: PROBLEMS AND SOLUTIONS

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Disposal of solid waste from blue crab processing plants became a major problem in Maryland with the closing of dehydrating plants. The dehydrated crab waste (scrap) was ground and sold for chicken feed. Presently, the scrap is disposed of in landfills; however, risk of ground water pollution and operational problems of placing crab scrap in landfills limits landfilling to a temporary solution. Composting of the crab scrap is a possible method of stablizing the waste and producing a useful soil additive for farmers, gardeners, the potted-plant industry, and others. Composting of crab scrap requires special provisions to eliminate noxious odors and prevent nuisance problems from developing. Studies to date have shown that the crab scrap pH must be maintained below 7.5 during composting, aeration must be supplied during part of the composting cycle, and a source of additional carbon must be added to the scrap. Solutions to these problems and methods of composting have been developed which produce high quality compost without noxious odor production.

OPTIMUM SALINITY REGIME FOR OYSTER PRODUCTION ON LOUISIANA'S STATE SEED GROUNDS

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Increased salinities have drastically reduced the productive portion of Louisiana's public oyster seed grounds. Controlled freshwater diversions from the Mississippi River have been utilized or are now being planned in an attempt to reduce salinities and thereby reestablish formerly productive reefs. These diversions offer an unprecedented opportunity to manipulate salinities over a vast estuarine area for maximizing seed oyster production. The purpose of this study was to determine the optimum annual salinity regime, using historical data, for the production of seed oysters on Louisiana's seed grounds.

Salinity, spatfall, and seed oyster production data from three stations on Louisiana's productive seed grounds, 1971–1981, are presented. Salinity in the setting year was the prime factor determining production of seed oysters. Both high and low salinity extremes resulted in poor seed production. Insufficient setting was blamed for poor production at the low salinities and it was speculated that numerous organisms associated with the high salinities caused heavy mortalities in recently set oysters. The optimum annual salinity regime was derived from all of the year/station salinity regimes which were followed in the ensuing year by good seed oyster production. This optimum regime accounts for the salinity dependent factors which limit seed production.

GENE STRUCTURES OF ATLANTIC COAST POPULATIONS OF THE BLUE CRAB *CALLINECTES SAPIDUS* RATHBUN

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Recent research has indicated that larvae of blue crabs are probably flushed from their parent estuary. Development continues in offshore waters, after which late-stage larvae or post-larvae return to the estuaries. A genetic study of blue crab populations was undertaken to determine if there is sufficient gene exchange among estuaries to prevent differentiation. Horizontal starch-gel techniques were used. Statistical analyses of frequencies of polymorphic loci indicate that blue crab populations south of Cape Hatteras are more genetically similar to each other than to those north of that cape.

NATICID SNAIL PREDATION IN NEW ENGLAND: THE EFFECTS OF *LUNATIA HEROS* ON THE POPULATION DYNAMICS OF *MYA ARENARIA* AND *MACOMA BALTHICA*

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The naticid snail predator *Lunatia heros* (Say) and two of its bivalve prey species, *Mya arenaria* Linné and *Macoma balthica* (Linné), were studied at an intertidal site in eastern Maine. The *M. arenaria* population was comprised largely of newly recruited individuals. Survivorship was low (3.5%/y) until the sixth year and increased thereafter. *Lunatia heros* preyed upon only those individuals of *M. arenaria* < 30 mm long. At that length the bivalve reached a size or depth refuge from predation. It delayed reproduction until it was 4 years old (20 mm long) and allocated its resources to rapid early growth instead (4.9 mm/y for the first 5 y).

The dynamics of the population of *M. balthica* were different. There was a larger proportion of older individuals of *M. balthica*, and survivorship was higher (76.3%/y for the first 5 y). *Macoma balthica* grew to a length of 25 mm and never reached a size refuge. All sizes were susceptible to attack by *L. heros*, but the deeper burrow of *M. balthica* relative to individuals of *M. arenaria* of the same size may have afforded it some protection from predation. *Macoma balthica* grew slowly (2.7 mm/y for the first 5 y) and diverted its resources into reproduction at a younger age (3 y) and smaller size (10 mm). These different life-history patterns and the possible relationship between bivalve resource allocation and refuges from predation are discussed.

THE EFFECTS OF POLLUTANTS ON LARVAL DEVELOPMENT OF THE BLUE CRAB *CALLINECTES SAPIDUS* RATHBUN

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Since our initial rearing of all larval stages of the blue crab *Callinectes sapidus* from hatching to the juvenile crab, we have investigated the way in which a variety of pollutants may affect the survival, duration, and frequency of abnormality of larvae of this important commercial species. Having established the optimum temperatures and salinities required for total development, we have investigated the way in which a number of commonly used pesticides and heavy metals affect development, either singly or in combination with those temperatures and salinities which are known to impose a stress on the developing larvae. Included among

the pesticides have been studies on Malathion, Methoxychlor, Mirex, Kepone, and Dimilin. Studies on the effects of heavy metals have included cadmium and mercury.

Summary data involving these studies are presented and discussed. In all cases, small amounts of each of the chemicals tested reduced survival of the larvae. Even at "sublethal" levels, abnormalities in development were observed. In general, the larval stages were far more sensitive to pollutants than were the juvenile or adult crabs and any consideration of "water quality" should take into consideration this essential portion of the life cycle of the blue crab and the sensitivity of the various larval stages to extremely minute amounts of pollutants.

ANALYSIS OF LOCAL POPULATIONS OF THE BLUE CRAB *CALLINECTES SAPIDUS* RATHBUN

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The catch of blue crabs and composition of that catch fluctuate rapidly and widely over time. Useful estimation of local availability, size structure, and sex composition is, however, essential for understanding and for management of the species. A procedure of obtaining such information is described and discussed. It involves detailed catch information from the best of samplers (selected professional crabbers) accompanied by appropriate quantitative observation at frequent intervals on the composition of the catch. These can provide useful estimates of the number of each class of crab available per man day throughout the crabbing season. The advantage and limitations are considered.

CHEMORECEPTION AND LIFE HISTORY OF *STYLOCHUS ELLIPTICUS* (GIRARD)

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Stylochus ellipticus, a flatworm indigenous to the Atlantic coast of the United States, preys on oyster spat and barnacles. Adults have almost inflexible prey preferences. Little is known about early life stages. A prey chemolocation hypothesis was tested to explain ability of *S. ellipticus* to locate and discriminate prey species. Also, these studies initiated examination of life history and distribution of *S. ellipticus* in Chesapeake Bay.

Three apparatuses (chemossayer, Y-maze, and choice-chambers) were used to test adults for chemoreception. Effects of various environmental and biotic factors on chemoreception were tested. The Atlantic oyster drill *Urosalpinx*

cinerea (Say), an ecological analogue with an extensively studied chemobiology, was used to verify apparatus effectiveness and stimulus and control water attractiveness. Survivorship of larvae in nutrition and substrate preference settlement studies was determined. Distribution of *S. ellipticus* in Chesapeake Bay was determined from oyster bar survey reports (1980–81), occurrence in oyster hatcheries (1980–81), and prior fouling plate studies (1963–65) (Shaw 1967).

Studies of *U. cinerea* verified effectiveness of apparatuses and of stimulus and control water. Chemoreceptive behavior was indicated only in choice-chamber studies as long response time of adults rendered other apparatuses ineffective. Light and starvation modified prey search. *Stylochus ellipticus* has a Götte's larva which appears to be non-feeding and metamorphoses only on prey substrates. Though flatworm and prey densities often correlate, there were several instances of uninfested prey populations.

Adults of *S. ellipticus* appear to prioritize behavior: (1) reproduction vs. prey search, and (2) prey search vs. escape. Barriers to larval dispersal probably allow some prey populations to escape infestation. Earlier, nonreproductive life stages may influence prey preference establishment.

EFFECT OF CRAB POT WIRE TREATMENT ON CRAB POT FOULING IN CHESAPEAKE BAY, MARYLAND

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It has been presumed that fouling on crab pots reduces the catch rate and contributes to a shortened fishing life or premature loss of the pot. Groups of standard anode pots, standard anode pots painted with an anti-fouling paint, and vinyl pots were compared for rate of fouling and catch. Crab pots treated with the anti-fouling paint fouled the least. Their fouling rate was 83% less than vinyl pots and 75% less than standard anode pots. Pots treated with anti-fouling paint accounted for 42% of the total crabs caught during the study. This study suggests that treatment of standard anode pots with anti-fouling paint could increase not only catch, but also pot life.

AN OYSTER CULTCH COMPARISON: CLAMSHELL VS. LIMESTONE

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On 15 April 1981 four 70- × 70-cm trays containing equal

volumes of clamshell and graded crushed limestone were placed on the bottom at each of 10 stations in the Barataria Bay system of southeast Louisiana. At the end of 3 months two trays and their contents from each station were retrieved and replaced with two trays containing fresh material. After the following three months all trays were retrieved. Thus, the cultch materials were exposed to spat set for two successive 3-month periods and for one 6-month period. Spat set (spat/liter of cultch) was determined by counting live and dead spat on each piece of cultch material. The overall mean spat set/liter was 57.9 for limestone and 25.1 for clamshell. This ratio of approximately 2:1 also held true when the data were analyzed for each time period. Relative survival was slightly higher on clamshell; however, because of the greater set on limestone, there was still approximately twice the number of live spat on limestone as on clamshell. At current prices crushed limestone is approximately 60% higher than clamshell; however, since spat set on limestone was greater, the cost, using average prices, was about $0.50/1,000 spat on limestone and $0.70/1,000 on clamshell.

INCIDENCE OF PATHOGENIC BACTERIA IN THE BLUE CRAB *CALLINECTES SAPIDUS* RATHBUN AND THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN)

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Blue crabs (*Callinectes sapidus*) and American oysters (*Crassostrea virginica*) were analyzed for the presence of human pathogenic bacteria. Live and cooked crabs, freshly picked crabmeat, and live, shucked, and washed oysters were obtained from a Maryland processing plant in the winter and spring of 1981–82. Cans of pasteurized crabmeat, purchased in Washington, DC, area stores, were also included in the study. All samples were subjected to standard plate-count determination and enrichment for the detection of specific pathogens. Sample analyses revealed low numbers of *Staphylococcus aureus* Rosenbach, *Vibrio parahaemolyticus* (Fujino et al.), other halophilic *Vibrio* spp., *Aeromonas hydrophila* (Chester), fecal coliforms, and presumptive *Clostridium perfringens* (Veillon and Zuber) spores; *Vibrio cholerae* Pacini and *Salmonella* spp. were not detected. Excluding *S. aureus*, all of the pathogens were present in highest numbers in the live crabs and oysters, suggesting that processing is effective in controlling the numbers of pathogens present in these foods.

PREDATION ON SPAT OF THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN) BY THE AMERICAN LOBSTER *HOMARUS AMERICANUS* MILNE-EDWARDS, THE ROCK CRAB *CANCER IRRORATUS* (SAY), AND THE MUD CRAB *NEOPANOPE SAYI* (SMITH)

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Predation by lobsters, rock crabs, and mud crabs on oyster spat was compared in the laboratory at 13°C. Rock crabs (32- to 107-mm carapace width, CW) preyed on oysters up to 30 mm length, although they preferred smaller oysters. Preferred prey size increased with rock crab size. Lobsters (55- to 98-mm carapace length) demonstrated a broad preference for oysters of 10- to 25-mm length. Oysters up to 35-mm length were vulnerable to the lobsters. Predation rate was highly variable but generally increased with predator size. Maximum mean lobster and rock crab predation rates were 4.5 and 28.0 oysters/predator/day, respectively. Mud crabs (14- to 23-mm CW) and rock crabs (32- to 58-mm CW) feeding on oysters (2- to 9-mm length) attached to spat collectors ate approximately 0.5 oyster/predator/day.

Lobsters used their mouthparts or chelae to open oysters by indiscriminate crushing. Rock crabs generally crushed the umbo, chipped away the shell margin, or punctured the prey shell. Mud crabs and rock crabs opened oysters still attached to the spat collector. Oyster fragments were found in the stomachs of 88 (44%) of 201 rock crabs collected around oyster beds in Caraquet Bay, New Brunswick.

SEASONAL OCCURRENCE OF THE LARVAE OF *CALLINECTES SAPIDUS* RATHBUN IN DELAWARE BAY

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Blue crab larvae were collected weekly at a station in the mouth of Delaware Bay over a 16-wk period beginning in late June 1979. Collections were made with a 0.3-m Clark-Bumpus Sampler; discrete samples were taken at the surface, at 12 m, and at the bottom (25 m). On each sampling date, larvae were collected at the three depths every 3 h over one

tidal cycle. Only Stage I zoeae and megalopae were collected during the course of the investigation. Peak abundance of Stage I occurred during late July and early August while peak occurrence of megalopae was observed 5 wk later. Stage I larvae were most abundant in seaward-flowing surface water and megalopae were distributed throughout the water column. We concluded that blue crab larvae are exported from the Bay as Stage I zoeae, undergo subsequent zoeal development on the continental shelf, and return to the estuary as megalopae.

CHARACTERISTICS OF FECAL RIBBONS FROM JUVENILES OF *CRASSOSTREA VIRGINICA* (GMELIN) FED *PHAEODACTYLUM TRICORNUTUM* BOHLIN WITH AND WITHOUT THE ADDITION OF SILT: PRELIMINARY OBSERVATIONS

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Two size classes of *Crassostrea virginica* were fed *Phaeodactylum tricornutum* at two cell concentrations with and without the addition of silt. The experimental treatments included 3-g and 21-g oysters, algal concentrations of 1.0 $\times$ 10^4 cells/ml and 1.0 $\times$ 10^5 cells/ml, and either natural or oxidized Broadkill River silt at a concentration of 50 mg/ℓ. Each treatment was tested in replicate feeding trials lasting 24 h. Microscopic examination of fecal ribbon contents from oysters fed at the low algal concentration showed that the addition of silt resulted in a marked reduction in the number of whole cells of *P. tricornutum*. At the higher algal concentration the addition of silt had no effect on reducing the number of whole cells in the fecal ribbons. No differences in the effect were found between oyster size classes. SEM examination of all fecal material indicated that silt-treated samples were different in appearance and composition from those fed algae alone. The implications of silt additions in improving the nutritive value of *P. tricornutum* are discussed.

HEAVY METAL, POLYCHLORINATED BIPHENYL, AND PESTICIDE LEVELS IN *CRASSOSTREA VIRGINICA* (GMELIN) FROM CHESAPEAKE BAY

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Adult of *Crassostrea virginica* were collected from 51 sites in Chesapeake Bay and its tributaries. Samples were analyzed for heavy metal, polychlorinated biphenyl (PCB), and pesticide contamination. Ranges, medians, means, and standard deviations were determined for the Maryland portion of Chesapeake Bay and for some major river systems. Trends indicated by the 1980 data are discussed. Data are compared to previously collected data.

REDUCTION OF DISSOLVED ORGANICS IN BLUE CRAB PROCESSING PLANT EFFLUENT

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Blue crab processing plants have difficulty meeting discharge guidelines for federal and Maryland state liquid effluents. Conventional treatment systems (e.g., foam flotation or aerated lagoons) do not represent viable options because of severe land and cost constraints. Research was initiated to develop: 1) a cost effective effluent treatment system and 2) a system producing effluent of sufficient quality to meet discharge guidelines. An attempt was made to utilize ultraviolet light as a substitute for chlorination. Crab cooking retort water, diluted to a 5% strength, was used as a consistent feed solution containing a high level of dissolved organics. Chemical floculation (with aluminum sulfate, ferric chloride, or ferrous sulfate), foam fractionation, and aerobic biological treatment were examined in the laboratory using this solution to determine the most promising treatment method. Because of the high dissolved organics concentration in the effluent, aerobic biological treatment proved to be the most effective treatment method. Various retention times in a sequential biological reactor were studied. A significant reduction in dissolved organic concentrations was achieved, but substantial concentrations of colloidal particulates were produced. Filtration with a fine sand filter greatly reduced the particulate concentrations. Final polishing by activated carbon absorption produced effluent transmission values in the range necessary for effective disinfection by ultraviolet light. Water quality parameters were monitored between each treatment step. The quality of the water leaving the scale model system met federal and Maryland state discharge limitations.

MORPHOMETRIC PATTERNS IN INTERTIDAL BIVALVES

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For several families of intertidal gastropods Vermeij (1973) has demonstrated low-to-high shore gradients in shell morphology which he interpreted in terms of adaptive responses to the dominant physical stresses of the shore environment. Evidence from a variety of studies suggests that similar responses may occur in bivalves. The present study examined this question further. Juveniles of six bivalve species (*Argopecten irradians* [Lamarck], *Modiolus modiolus* [Linné], *Ostrea edulis* Linné, *Mytilus edulis* Linné, *Crassostrea virginica* [Gmelin], and *Geukensia demissa* [Dillwyn]) were grown at various tidal levels on a natural shore and in a laboratory tidal simulator. At the end of the treatment period, the bivalves were sacrificed and each specimen was measured for maximum shell dimension (MSD: length in the mussels, height in the other species) and width; dry meat and dry shell weights were also determined. Three morphometric ratios were calculated and compared among species and treatment groups: shell weight/(MSD × width) as an index of relative shell thickness; MSD/width as an index of relative shell globosity; and meat weight/shell weight. Bivalves that were grown intertidally tended to have thicker and more globose shells. These tendencies did not necessarily correlate with naturally occurring or experimental intertidal levels. Intertidal meat/shell ratios, however, corresponded closely to natural shore position; the lower-shore species had the lowest ratios and the higher-shore species had the highest. We concluded that inter-specific and, in some cases, intra-specific low-to-high shore gradients in morphometric relationships are present in bivalves.

NONPLANKTOTROPHIC LARVAL DEVELOPMENT OF TWO SPECIES OF CONTINENTAL SHELF BIVALVES

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Larvae of *Periploma leanum* (Conrad) and *Astarte castanea* (Say) were reared under laboratory conditions. The larval stages of both species are lecithotrophic and have low dispersal capabilities. Spawning was induced in *P. leanum* with thermal stimulation and the addition of a gamete suspension following a period of intensive feeding. Individual eggs (dia. $\cong$ 130 μm) were released inside of two-layered capsules. The outer gelatinous layer rapidly expanded and, within 24 hours, completely dissipated. After 4 to 6 days,

straight-hinge larvae emerged from an opening at the restricted end of the inner capsule. After a planktic stage of < 24 h, the larvae (length $\cong$ 170 μm) assumed an inactive benthic existence; a functional foot was not observed until 15 to 18 days after fertilization. At no time during larval or early postlarval development were byssal threads observed. *Astarte castanea* was induced to spawn with thermal stimulation and the addition of a gamete suspension. Individual eggs (dia. $\cong$ 170 μm) were released inside of double-walled, adhesive capsules. Prodissoconch I formation was extremely slow. The first sign of valve formation was observed after 6 to 10 days while the larvae rotated within the capsules. Movement within the capsule ceased between 8 and 15 days after fertilization when the valves first completely enclosed the soft tissues and closed against one another along their free margins. Between 22 and 26 days, young of *A. castanea* broke out of their capsules by pushing forcefully with their foot against the inner wall of the capsule. They emerged as benthic juveniles (ln. $\cong$ 240 μm). As a result of the adhesive nature of the encapsulated stages, the larval dispersal capability of this species is estimated to be on the order of a few centimeters.

THE ROLE OF THE VENTRAL PEDAL GLAND IN FORMATION OF AN EGG CAPSULE BY THE MURICID GASTROPOD *EUPLEURA CAUDATA ETTERAE* B. B. BAKER 1951: AN INTEGRATED BEHAVIORAL, MORPHOLOGICAL, AND HISTOCHEMICAL STUDY

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Several researchers described formation of egg capsules by females of a few neogastropods, but this process is still not well understood. Spawning behavior of females defined discrete times to sample egg capsules and spawning females before ventral pedal gland activity (VPGA), after peristaltic molding during VPGA, and after VPGA. Structure of these egg capsules and ventral pedal glands of females was examined with dissections, histology, polarizing microscopy, and histochemistry. Egg capsules before VPGA were ovoid, soft, and flexible. After peristaltic molding during VPGA, egg capsules were roughly shaped, loosely attached to a hard substratum, and still soft and flexible. Egg capsules after VPGA were completely shaped, firmly attached to a hard substratum, but now hardened and resilient. The apical plug, embryo chamber, and multilayered fibrous wall of egg capsules before, during and after VPGA had similar

morphologies. Histochemical composition of the wall of egg capsules before VPGA and after peristaltic molding during VPGA differed from that of the wall of the egg capsules after VPGA. The wall of whole egg capsules that were sampled before VPGA and exposed to filtered seawater for 5 days were soft, flexible, and showed no histochemical changes. These observations suggested that the ventral pedal gland molded an egg capsule into its final species-specific shape, firmly attached it to a hard substratum, chemically hardened the wall of the egg capsule, but did not secrete any layers of its wall. The ventral pedal gland has a columnar epithelium, two types of epithelial goblet cells, clusters of subepithelial gland cells, and a thin layer of circular and longitudinal muscle fibers between the epithelium and these gland cells. Each goblet cell type secreted different sulfated, acid mucosubstances that may act as lubricants during molding of egg capsules. Subepithelial gland cells may secrete a noncarbohydrate, nonprotein substance that hardens the wall of the egg capsule.

SOME RELATIONSHIPS AFFECTING GROWTH OF SEED OF THE HARD CLAM *MERCENARIA MERCENARIA* IN RACEWAYS

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Seed clams ($\bar{y}$ size = 3.9 mm) were maintained in raceways for 6 months at densities corresponding to 740, 2220, 6660, and 19980 clams/m^2. Each density was replicated eight times in the raceways and the highest and lowest densities were replicated four times in subtidal field controls. Raceway clam populations were stocked in four different positions relative to water flow and in 19 different positions relative to total raceway biomass. Although nominal flow rate was constant, effective flow rate (water volume/clam volume/minute) was different for each replicate and decreased as clam biomass increased. Temperature and salinity were measured daily and inflow and outflow chlorophyll-a were monitored monthly from February to August 1981 to determine growth and survival. Single classification ANOVA followed by SNK tests between means showed that growth was significantly reduced at the highest density in both the raceway and the field. The lowest density exhibited greater growth in the raceway than in the field, while the highest density showed no difference in growth between the two locations. In the raceway, growth rate was inversely proportional to distance from water inflow and to effective density

(# clams/unit water). Although clams at the highest density consistently removed the greatest amount of chlorophyll-a, less chlorophyll was removed per clam as density increased. Growth was highly correlated with stripping rate (μg chlorophyll-a/clam/day) and with effective water flow rate. These relationships are discussed and some implications for management of raceways in mariculture systems are made.

MIXED-FUNCTION-OXYGENASE ENZYME SYSTEMS: PURPOSE AND POSSIBLE DELETERIOUS INTER-ACTIONS WITH ORGANIC POLLUTANTS IN THE BLUE CRAB

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Mixed-function-oxygenases (MFO) are enzyme systems which have evolved in organisms to enable them to eliminate foreign compounds taken in from their environment. Often these compounds are toxic and lipophilic, possessing high accumulative potential (e.g., polynuclear aromatics, polychlorinated biphenyls, and chlorinated organic pesticides); therefore, they must be metabolized to biologically inactive, excretable forms. Occasionally, however, the resulting metabolites formed by the MFO system are more harmful than the parent compounds; some are potent carcinogens. Recent work has shown that the activity of the MFO system is greatest in mammals and decreases in fish, crustaceans, and mollusks, in that order. The enzyme system is also responsible for the synthesis and breakdown of certain steroid hormones. The molting hormone in crustaceans is believed to be a steroid compound. The activity of MFO in female blue crabs has been shown by others to be inversely related to the levels of crustecdysone, when examined over the course of a molt cycle. Elevated levels of aromatic hydrocarbons, caused by greater utilization of coal reserves and increased industrialization, are of concern to scientists. These and other pollutants have been found by workers to induce higher levels of MFO activity, and also to inhibit molting and limb regeneration in crabs. Levels of toxic organic compounds in the blue crab population of lower Chesapeake Bay are being determined using glass capillary gas chromatography and mass spectrometry. Differential abilities to metabolize aromatic compounds that may exist between molt and sex groups will be examined.

ESTIMATES OF JUVENILE BLUE CRAB ABUNDANCE IN TEXAS BAYS

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Blue crab populations were monitored November 1977–December 1981 by Texas Parks and Wildlife Department personnel using 18-m bag seines in the Galveston, Matagorda, San Antonio, Aransas, Corpus Christi, upper and lower Laguna Madre Bay systems. Seine samples and hydrological data were taken monthly at randomly selected stations in each of the sampled bay systems. Catch-per-unit-of-effort (CPUE), calculated as number of crabs/ha, as well as water temperature and salinity values are presented. These data were examined utilizing a 2-way ANOVA. Similarities in CPUE, water temperature, and salinity were examined between years and seasons within bay systems.

THE SURF CLAM ALONG THE NEW JERSEY COAST: POPULATION SIZE, RECRUITMENT, GROWTH RATES

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Over the last 10 years there has been regular and general settling of surf clam larvae along the New Jersey coast but, as indicated in earlier reports, mortality rates in early juveniles are high and survival beyond the first summer is comparatively rare. Exceptions to this will be discussed with emphasis on the 1976 year class which approximately doubled the standing stock in New Jersey waters. Since major portions of this year-class survived in areas where earlier year-classes were wiped out by anoxic waters in 1976, we have a unique opportunity to determine the effects of a variety of environmental conditions on growth rate. Results of some of these determinations will be presented, as will the most recent stock assessment.

GROWTH PERFORMANCE OF CYTOCHALAZIN-INDUCED TRIPLOIDS OF AMERICAN OYSTERS AND SOFT-SHELL CLAMS

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We conducted extensive laboratory and field performance experiments in 1982 with 3-yr-old triploids of the American oyster *Crassostrea virginica* (Gmelin) and yearlings of the soft-shell clam *Mya arenaria* Linné. The *Crassostrea* triploids, which were created at meiosis 1, grew significantly faster than the diploid controls, whereas those created later in the meiotic cycle exhibited no growth advantage over the dip-loids. The *Mya* triploids exhibited no growth advantage over diploid controls. Triploidy did not block gametogenesis in either species. Optimal methods are discussed for determining the consequences of polyploidy in marine bivalves.

PREDATION BY BLUE CRABS AND SPOT ON INFAUNAL COMMUNITIES IN CENTRAL CHESAPEAKE BAY

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The impacts of predation by blue crabs (*Callinectes sapidus* Rathbun) and spot (*Leiostomus xanthurus* Lacepède) on infaunal communities were compared for mud and sand sediments in the Rhode River, a typical subestuary of central Chesapeake Bay. The two species are the dominant benthic predators in the system, and their foraging activities from June to October correlated with the sharp seasonal decline in infaunal density and standing crop. Analysis of stomach contents showed that crabs preyed primarily on whole clams, whereas spot fed mainly on clam siphons and several species of polychaetes. Turnover rates of infaunal prey were estimated based on the density of predators taken in otter trawls, the weight of their stomach contents, and the weight of the standing crop of infauna. For total infauna, turnover rates were low (1–7%/month) early in the season, when the standing crop was high; but turnover was high (30–60%/mo) in the top 5 cm of sediment late in the season, when the standing crop was low. For small clams, polychaetes, and amphipods in the top 5 cm of sediment, predation pressure by crabs and spot accounted for extremely high turnover rates (more than 100%/mo), whereas larger, deep-burrowing clams had turnover rates < 3%/mo. Experiments using predator exclusion cages resulted in significantly higher densities of total infauna, clams, and some species of polychaetes within the cages than outside the cages. Survival of out-planted clams (*Macoma balthica* [Linné]) was significantly higher in buckets with predator exclusion cages than in buckets without predator exclusion cages. Predation by blue crabs appears to have a major impact on small, surface-dwelling clams, whereas spot predation has a more general impact on clam siphons and a variety of invertebrates living in the surface sediment. Turnover of infauna in the surface sediment is very rapid.

OCEANOGRAPHY OF THE SOUTHEASTERN BERING SEA AND RECRUITMENT PROCESSES IN TWO SPECIES OF TANNER CRAB

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Potential factors affecting the distribution and survival of the pelagic larvae of two species of tanner crabs, *Chionoecetes bairdi* Rathbun and *C. opilio* (Fabricius), that inhabit the wide continental shelf of the eastern Bering Sea were investigated as part of a large multi-institutional oceanographic program. The objective was to evaluate the relative importance of pelagic events in determining spatial patterns of recruitment to the benthos. The study emphasized the description of cause-and-effect relationships between physical processes (mixing and transport) and biological (planktonic) conditions which affect feeding success and the ultimate survival and distribution of the larvae. Information on the timing of hatch-out, rates of growth and development, feeding physiology, and inter-annual differences in patterns of spatial distribution and relative abundance of the larvae are provided. How these data relate to regional oceanographic processes and their potential impact on population distribution and age structure are stressed.

SPECIES-SPECIFIC DIFFERENCES IN THE MEGALOPAL DISTRIBUTIONS RELATED TO WATER DENSITY PARAMETERS

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The megalopae of 10 brachyuran crabs were sampled from July through September 1980 in the lower Chesapeake Bay and adjacent coastal waters. The megalopae are assigned to three apparent groups: retained estuarine, expelled estuarine, and retained coastal recruitment types. The megalopae of estuarine species such as *Hexapanopeus angustifrons* (Benedict and Rathbun), *Neopanope sayi* (Smith), *Panopeus herbstii* H. Milne-Edwards, and *Pinnotheres ostreum* Say are retained in estuarine epibenthic waters. The larvae of some estuarine species such as *Callinectes sapidus* Rathbun, *Uca* spp., and *Pinnixa* spp. are expelled from the estuary, resulting in maximum megalopal concentrations on the shelf. Of the retained coastal species, *Portunus* spp. and *Cancer irroratus* Say are not abundant in the neuston of shelf waters, while *Libinia* spp. are most abundant in the epibenthos of near-shelf waters. The megalopae of 4 species show significantly different vertical distributions between stratified and homogenous water columns. Megalopae were not found to aggregate within pycnoclines.

MECHANISM OF SHELL PENETRATION BY THE BURROWING BARNACLE *TRYPETESA LAMPAS* (HANCOCK), (CIRRIPEDIA: ACROTHORACICA): AN ULTRASTRUCTURAL STUDY

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Trypetesa lampas is a soft-bodied, free-living cirriped that burrows in empty shells of gastropods inhabited by hermit crabs. Portions of this burrow are commonly lined with a limy, white material. Individuals of *T. lampas* were obtained from shells of *Lunatia heros* (Say) and *Polinices duplicatus* (Say) collected in the vicinity of Woods Hole, Massachusetts. Specimens of the mantle surface and burrow wall were examined with scanning electron microscopy to determine the mechanisms of shell removal and lining formation within the burrow by *T. lampas* and to correlate these activities with the microanatomy of the external mantle surface of the barnacle. Results confirm earlier hypotheses that burrowing by *T. lampas* is achieved through a combination of chemical and physical processes. Ultrastructural examination of fractures through the burrow reveal a gradual, shell-weakening process in which prismatic material within the surrounding gastropod shell is softened by preferential dissolution of inter- and intra-crystalline matrix and subsequent solubilization of the bare calcareous prisms. Examination of thin sections through the mantle cuticle disclosed minute pore canals through which shell-dissolving secretions of the barnacle could be released. Dissolution of shell by *T. lampas* appears to be linked to the molt cycle, with most extensive stages of dissolution being observed in burrows of specimens that have just molted. Soft material remaining on the wall of the burrow after molting is removed with sharp spines covering the external surface of the barnacle's mantle. This material is subsequently used by *T. lampas* to thicken existing parts of the lining and add new linings in areas that no longer fit snugly.

TRACE METALS IN SHELLFISH AND GROWING AREA DESIGNATION

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The level of coliform bacteria, as set forth by the National Shellfish Sanitation Program (NSSP), is the water quality

standard used to classify shellfish growing areas. It is the standard by which shellfish harvesting is regulated. Port Jefferson Harbor, NY, a moderately industrialized embayment of Long Island Sound, and Setauket Harbor, a more urbanized tributary basin of Port Jefferson Harbor, both have areas classified as certified (shellfishing permitted) and as uncertified (shellfish prohibited). Sediment analyses of the two harbors suggest that noncoliform pollutants, particularly trace metals, are present. Because of public health concerns, the hard clam *Mercenaria mercenaria* (Linné) was sampled for trace metals to determine how trace metal concentrations in the shellfish tissues compared with the level of bacteriological pollution in the growing water and the NSSP classification. Hard clams were sampled from 5 locations in each harbor and analyzed for copper, lead, zinc, and cadmium. From the metal and coliform concentrations and their distributions in the two harbors, the following relationships were observed: in both harbors, hard clams from the station with the fewest coliform bacteria did not have the lowest metal concentrations; in Setauket, the variability in metal concentrations among the sampling locations was much less than in Port Jefferson; and in Port Jefferson, overall metal concentrations were higher than in Setauket. The concentration of metals in the shellfish does not appear to be reliably related to the coliform level.

BLUE CRAB PREDATION ON INFAUNAL BIVALVES: RELATION TO OPTIMAL FORAGING HYPOTHESES

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Adult blue crabs (*Callinectes sapidus* Rathbun) were allowed to forage on equal numbers of 3 size classes of buried soft-shell clams (*Mya arenaria* Linné); percentage of clams ingested increased with increasing clam size. This was also true in the case of juvenile blue crabs foraging on equal numbers of 5 size classes of buried specimens of *Macoma balthica* (Linné). When the largest size class of *M. balthica* was not available and equal numbers of the four remaining size classes could be preyed upon by juvenile crabs, the percentage of clams ingested increased with increasing clam size. This seems to indicate a pattern of optimal foraging by the crabs. Equal biomass of (a) two size classes of buried specimens of *M. arenaria* or (b) three size classes of buried specimens of *M. balthica* was then made available to adult or juvenile blue crabs, respectively. At the end of these experiments there was no statistically significant difference among size classes in percentage of clams ingested. This suggests that buried clams are preyed upon opportunis-

tically by blue crabs. The results of the experiments using equal numbers of clams per class may have been influenced by the possibility that larger clams have a greater chance than smaller clams of being encountered by a sediment-probing crab because of their larger size.

DEPARTMENT OF NATURAL RESOURCES AND UNIVERSITY OF MARYLAND FORM NEW COOPERATIVE SHELLFISH RESEARCH UNIT AT CRISFIELD

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The University of Maryland's Marine Products Laboratory located at Crisfield has become the site of a joint University/Department of Natural Resources (DNR) program in shellfish management effective 1 January 1982. The new joint research and management program will offer many advantages to the state's seafood industry by combining research and management functions in one unit as well as providing for the transfer of new hatchery technology through demonstrations of shellfish culture methods to watermen, seafood processors, and other interested groups.

THREE INNOVATIVE TECHNIQUES THAT MADE MARYLAND OYSTER HATCHERIES COST-EFFECTIVE

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The combined use of 3 innovative techniques reduced the size of the physical plant of a Maryland oyster hatchery by 65% and reduced the labor by 55%. Tahitian *Isochrysis*, an unidentified algal strain that has an optimal growth temperature between 24 and 30°C, eliminated the need for a temperature controlled algae culture room in the hatchery. Algae cultures were grown at ambient room temperature and stored in a "concentrated paste" after dewatering in a mechanical centrifuge. This technique permitted year round operation of a small algae culture laboratory rather than an intensive period of activity during the time of oyster larval culture (June through August). Oyster spat were collected directly from larval culture cones on a concrete-coated, wire device which also served as a growing substrate until the spat reached 2.5 to 3.5 cm. This growing device was transferred directly from the larval cone into the natural environment thereby eliminating the need for continuous flow of water in the hatchery and the labor involved with cleaning vast expanses of spat culture trays. Field trials of spat grown by

these techniques will yield marketable oysters in the fall of 1983.

EFFECT OF PROCESSING ON STEROL AND FATTY ACID COMPOSITION OF CRABMEAT

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The use of water or brine or mechanical stress for crabmeat extraction and the freezing or further heating of crabmeat for canning purposes are processing techniques employed by the crabmeat industry. The impact of physical and chemical processing is discussed relative to the effect on the lipid portion of the meat (primarily on the sterol and fatty acid composition). Specific processing techniques to be discussed include: freezing, multiple freeze/thaw cycles, canning (both sterilized and pasteurized and the inclusion of bacteria in the product after canning), and three methods for meat extraction.

ESTIMATION OF STANDING CROP OF *MERCENARIA MERCENARIA* (LINNÉ) IN THE JAMES RIVER, VIRGINIA, USING COMMERCIAL RECORDS

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Commercial catch and effort records for boats using patent tongs to harvest hard clams from the James River were obtained for the years 1978–1981. Using Dickie's (1955) version of the Leslie method, catch-per-unit-effort of the sample fleet was regressed against accumulated catch to give estimates of the initial abundance. Estimates for 1978, 1979, 1980, and 1981 were 10,101 m^3 (280,605 bu), 14,625 m^3 (406,250 bu), 20,065 m^3 (557,250 bu), 12,397 m^3 (344,364 bu), and 14,297 m^3 (397,142 bu), respectively. The mean for the period 1978–1981, 14,297 m^3 (397,142 bu), was 30% below that estimated by Haven et al. (1981). Commercial catch records can be used in this application but limitations in the data must be understood. Abundance estimates from this method should be supplemented with additional designed sampling strategies to give better accuracy.

EFFECTS OF LIGHT AND GRAVITY UPON THE MOTILE BEHAVIOR OF TROCHOPHORE LARVAE OF *MERCENARIA MERCENARIA* (LINNÉ)

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Adults of *Mercenaria mercenaria* were spawned in the laboratory and the fertilized eggs were reared to the trochophore stage. Responses of the larvae to light and gravity were observed. Distributions were determined under 5 experimental conditions: horizontal chamber in darkness, horizontal chamber with two different light intensities (2.5 and 15 W/M^2) shining from one end, vertical chamber in darkness, vertical chamber with light incident from above (2.5 W/M^2) and a vertical chamber with light incident from below (2.5 W/M^2). The results revealed a random distribution of the larvae in horizontal dark and horizontal light experiments, a substantial surface aggregation in the vertical dark chamber, and a decrease in surface accumulation with the light source shining from above and below the vertical chamber. Individual swimming paths of the larvae were analyzed using a computer-video system (viz., the Bug-system). The larvae were viewed in both the presence and absence of light in a vertical plane. Illumination from below caused a significant drop in vertical velocity and swimming speed and a small decline in the rate of change of direction. Phototaxis was not observed. Photostimulation caused the trochophores to exhibit a negative orthokinesis with a weakening in their negative geotactic behavior.

GROWTH OF JUVENILES OF *ARCTICA ISLANDICA* (LINNÉ) IN EXPERIMENTAL CONTAINERS

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Laboratory-reared ocean quahogs (*Arctica islandica*) (n = 119) ranging in shell length (maximum antero-posterior dimension) from 1.8 to 4.3 mm ($\bar{x}$ = 2.5 ± 0.4 mm, SD) were placed during June in experimental mesh containers suspended from fixed and floating structures in marine waters off Boothbay Harbor, Maine. Shell length measurements were recorded at monthly intervals until the following March. Water temperatures at the locations of the containers ranged from a high of 15.5°C during August to a low of 1.0°C during February. Mean growth rages recorded during the warmer months from June through September

ranged from 2.0 to 2.4 mm/month. Reduced, yet measurable, amounts of shell ($\bar{x}$ = 0.3 – 0.5 mm/month) were deposited during even the coldest winter months (January and February). Mortality during the study period was < 1%. By early March, the shell lengths of specimens (n = 117) ranged from 3.9 to 21.3 mm ($\bar{x}$ = 14.0 ± 2.8 mm, SD). Recorded growth rates were considerably faster than those heretofore reported for *Arctica islandica* and suggest that juveniles of this species have a potential for relatively rapid growth in certain environments.

SIZE AND VOLUME RELATIONSHIPS IN JUVENILES OF *MERCENARIA MERCENARIA* (LINNÉ): A REVISION OF BELDING'S TABLES

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Size and volume relationships in juveniles of the hard clam *Mercenaria mercenaria* were determined in commercial nursery populations over a 1-y period. Morphometric determinations included size (longest anterior-posterior dimension), displacement volume, and packed volume (wet). These data were used to establish empirical relationships between seed size and volume (displacement and wet packed) which are reported here as a revision of Belding's Tables. The empirical relationships, thus established, were iteratively employed in the construction of a model to predict seed clam volume. The model assumed that the volume of a hard clam is proportional to the cube of a linear dimension. The iterations allowed model refinements which produced positive correlations between predicted and observed data. We summarize collected data on size/volume relationships in seed clams and present a model, based on truncated spheres, which attempts to relate size and volume characteristics in seed clams within the size range of 1.0 to 15.0 mm.

A DESCRIPTIVE MODEL FOR THE CONSERVATION OF BLUE CRAB LARVAE IN THE VICINITY OF CHESAPEAKE BAY

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An extensive series of plankton samples taken from the waters around Chesapeake Bay indicates that all larval stages of the blue crab *Callinectes sapidus* Rathbun are concentrated in the upper layers of the water column with maximum numbers in the upper 1 m. This distribution insures that stage 1 larvae hatched near the bay mouth are entrained in the outwardly flowing surface water. The general longshore current in the Mid-Atlantic Bight is southward which would tend to transport larvae towards Cape Hatteras. This would result in their being lost to the system. Recent evidence suggests that during the summer months, when peak spawning occurs, there is a wind generated counter-current on the inner shelf. The width and speed of this corridor is related to wind direction and velocity. Larvae entrained in this counter-current are returned to the vicinity of Chesapeake Bay and contribute to recruitment. The horizontal distribution of blue crab larvae from field samples is consistent with this hypothesis.

A TEST OF A DART TAG FOR JUVENILE BLUE CRABS, *CALLINECTES SAPIDUS* RATHBUN

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A small dart tag was applied to the posterior junction between the ventral and dorsal parts of the cephalothorax of 80 juvenile blue crabs to test for success of molting and tag retention during the molting process. Sixty-one percent of tagged crabs which began ecdysis were successful in molting and retained the tag; however, overall mortality rate for tagged crabs was twice that of the untagged control group.

METHODS FOR FIELD EXPERIMENTS WITH BAITED TRAPS

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The number of uncontrolled variables and the number of potentially testable variables in the field environment can be distracting and intimidating to the field technicians. This environmental complexity requires greater mental discipline to conduct good experiments in the field than is required in the tidier laboratory environment. Problems frequently encountered in conducting experiments on design and fishing strategy of baited traps are as follows. Testing of hypotheses using fishermen's logbook data commonly gives biased results and has poor resolution because fishing variables are neither controlled nor random and data are often incorrect. Because most fishermen lack appreciation for correct experimental procedures, even dictating an experimental design will not assure a properly executed experiment. Preliminary

trapping should be carried out to locate an experimental area with uniform catch rates, to determine the optimum sample size, and to solve logistical problems in conducting the experiment. Experimental treatments should be randomized in space and time to avoid bias. An investigator rarely knows enough about the uncontrolled variables in the field to justify a systematic allocation of treatments in space and time. Variance is controlled by careful attention to details of bait quantity and quality, by keeping traps in good repair, by standardizing soak time, and by standardizing time of day of setting traps.

A FIRST ESTIMATE OF INDIRECT FISHING MORTALITY IN THE ICELAND SCALLOP *CHLAMYS ISLANDICA* (MÜLLER)

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Natural mortality in Iceland scallops (*Chlamys islandica*), computed from the ratio of cluckers to live animals, as might be expected, increased with age. Higher than average rates were found for the fully recruited ages (≥ 8 y) on heavily exploited grounds than in scallop beds subject to light or initial exploitation. The difference in mortality rates between near-virgin and fully exploited areas is ascribed to indirect fishing mortality associated with repetitive towing on productive grounds.

THE ANNUAL GLYCOGEN CYCLE IN THE SOFT-SHELL CLAM *MYA ARENARIA* LINNÉ FROM MAINE

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A field population of adults of *Mya arenaria* was sampled at approximately semi-monthly intervals for one year to determine glycogen levels in the meats. Highest levels occurred in late spring and early summer. Post-spawning late summer and fall levels were intermediate, and lowest levels occurred in the winter. Glycogen levels in juveniles and adults of *M. arenaria* were compared and the relationships between glycogen levels and gametogenesis, food availability, and temperature are discussed.

THE EFFECTS OF SEDIMENT TYPE ON GROWTH RATE AND SHELL ALLOMETRY IN THE SOFT-SHELL CLAM *MYA ARENARIA* LINNÉ

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Hatchery-reared juveniles of *Mya arenaria* were grown for 11 weeks in replicated gravel, sand, mud, and pearl net treatments under flow-through seawater conditions in Maine. Analyses of variance showed significant differences between sediment treatments for final shell length, dry meat weight, chondrophore growth increment, and percent shell weight. Growth of juveniles of *M. arenaria* was more rapid in fine sediments than in coarse sediments or nets. The slopes of shell length vs. shell height and shell length vs. shell depth regressions also varied significantly between sediment treatments. Slower growing clams from nets and gravel were more globose than clams from sand or mud treatments. Clams reared in sand were longer and narrower than those reared in mud. Differences in growth rates and shell form were attributed primarily to the physical properties of the substratum.

PREFERENTIAL INGESTION OF ORGANIC MATERIAL FROM THE CONSUMED RATION BY THE OYSTER *CRASSOSTREA VIRGINICA* (GMELIN)

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Considerable debate exists in the literature as to whether suspension-feeding bivalve molluscs can preferentially ingest the organic component of the seston. Most of those discussions were based on circumstantial evidence rather than reliable, quantitative measurements of the chemical composition of the oyster's food or biodeposits. This paper gives details of steady state measurements of the carbon, nitrogen, and energy content of the seston being fed to the oyster *Crassostrea virginica* and of the faeces and pseudofaeces being voided. The results indicate that, over the tested range of food concentrations (from 4–20 mg/l), the amount of energy (expressed as Joules/mg of dry weight of material) voided in the pseudofaeces by *C. virginica* can be reduced by 60% compared to the concentration in the food. Similar results were obtained from the carbon and nitrogen analysis. These data strongly indicate that *C. virginica* has the capability of selecting certain particles from the total seston filtered from suspension, with the result that more food particles are rejected in the pseudofaeces.

FACTORS LIMITING ABUNDANCE OF *CALLINECTES* SPP.

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The abundance of organisms varies in space and time because the factors that limit abundance vary spatially and temporally. Understanding limiting factors and the ways organisms respond to them can lead to improved blue crab catches. Blue crab populations can be limited directly by (1) insufficient recruitment from the plankton; (2) inadequate water quality, due either to natural or man-made causes; (3) insufficient resources, including food and cover; (4) interference competition, especially from other crabs; and (5) removal by parasites, natural predators, and crabbers. Each of these classes of limiting factors can be tested experimentally. The results of these studies can suggest more effective ways to improve catches by managing not only the populations of blue crabs, but also the ecosystems to which they belong.

TOTAL WIDTH-WEIGHT RELATIONSHIPS OF THE BLUE CRAB *CALLINECTES SAPIDUS* RATHBUN FROM THE ASHLEY RIVER, SOUTH CAROLINA

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Equations expressing total width-weight relationships of blue crabs (*Callinectes sapidus*) were calculated in relation to sex, sex by maturity, sex by molt sign, and sex by carapace form. All calculations were restricted to intermolt (Stage C) crabs except when molt sign was considered, and comparisons were restricted to crabs of similar size. Sex, maturity, molt sign, and carapace form significantly affected width-weight relationships. Overall, males were heavier than females of equal width. Mature males exhibited a greater mean weight than immature males, but mature females weighed less than immature females of similar size. Crabs with short lateral spines were heavier than those of the same sex with long spines. Intermolt and premolt (Stage D) males and females were heavier than recently molted (Stages A and B) males and females, respectively. Premolt females were heavier than intermolt females; a similar difference was not observed for males. Ashley River crabs were generally heavier than crabs from Florida, Texas, and Virginia. These differences may not be real, however, because many variables affect width-weight relationships of blue crabs and only sex differences were reported. Geographical variation is known to exist in crab populations, but only well defined comparisons between populations should be considered.

SIGNIFICANCE OF THE NEUSTON LAYER IN THE DISPERSAL OF LARVAE OF THE BLUE CRAB *CALLINECTES SAPIDUS* RATHBUN

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The distribution of larval blue crabs in the water column affects their transport out of Chesapeake Bay and during the larval period. The patterns of vertical distribution are not similar to those of other crab species in the region. First stage larvae are found predominantly in the neuston layer during the hatching season in the mouth of Chesapeake Bay and are carried seaward by the ebb tides. Later developmental stages, including the megalopae, are also found predominantly in the neuston or upper 1m, with very few being caught in intermediate layers or near bottom. Up to 99% of stage I larvae in the bay mouth and more than 70% of all *Callinectes* larvae of all stages even offshore were found above 1m. No evidence of vertical migration of any stage was obtained. The effect of this distribution is to make larval blue crabs very susceptible to surface effects and wind driven currents during larval development and immediately after metamorphosis to the megalops. Studies which do not include the neuston layer may overlook a major fraction of the total population of blue crab larvae. Most previous studies of larval blue crab occurrence and distribution did not include sampling of the neuston and consequently some conclusions based on those studies were erroneous.

GROWTH ENHANCEMENT OF *MYA ARENARIA* LINNÉ AND *MERCENARIA MERCENARIA* (LINNÉ) BY MARINE MACROALGAE

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Juveniles of *Mya* and *Mercenaria* were Alizarin-stained and cultured for 12 weeks in flow-through tanks containing one of three different species of macroalgae. Clams grown with *Ascophyllum nodosum* Linnaeus and *Laminaria longicruris* De la Pylaie were significantly larger with respect to shell dimensions than controls and those grown with *Ulva lactuca* Linnaeus. Maximum enhancement was observed with *Ascophyllum* in all cases; *Mya* grown with *Ascophyllum* grew 4.54 times more than controls, while *Laminaria* treated *Mya* showed 2.14 times more growth. A similar but less pronounced trend was seen for *Mercenaria*. Treatments with *Ascophyllum* and *Laminaria* were 12.6% and 9.6% larger than controls, respectively. Growth with *Ulva* was less

than control treatments but differences were not significant. The mechanisms of growth enhancement from different macroalgae and their importance in aquaculture are discussed.

ECONOMIC CONSIDERATIONS IN MANAGEMENT OF THE COMMERCIAL BLUE CRAB FISHERY

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From an economic prospective, the major consideration of common wealth fishery management is to maximize net benefits derived from the resource. In the case of commercial fisheries, net benefits accruing to society should include harvest revenues minus private costs (e.g., public administration and enforcement). In order to accomplish management objectives, private costs and public transactions costs need to be minimized. A simple review of various blue crab regulations germane to these economic concepts was performed.

CHEMICAL ECOLOGY OF OYSTER DRILLS

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Oyster Drills are predatory snails that eat a wide spectrum of shelled prey such as oysters, mussels, and barnacles. Drills have a well documented ability to locate intact prey from a distance by following chemical trails. We have looked in detail at the molecular basis of prey location by drills. Newly hatched drills can locate only barnacles from a distance. This ability is apparently genetic as maternal diet and prey odor environment do not enable the young to locate other prey such as oysters or mussels. Once a newly hatched drill has fed for some time on oysters, however, it develops the ability to locate oysters. The molecules used by drills to locate either barnacles or oysters are similar peptides. Animals that can locate only barnacles, however, cannot use even high concentrations of oyster attractant to locate oysters. Drills cannot locate mussels from a distance even if they have fed upon mussels. In fact, mussels produce a molecule that suppresses the ability of drills to locate prey from a distance. This molecule is much different than the attractant molecules. It has a molecular weight less than

500 Daltons and does not appear to be a peptide. As a result of the differences between attractants and suppressants and the responses of inexperienced versus experienced drills we can measure levels of attractants and suppressants in natural waters. We hope that an understanding of the molecules and mechanisms involved in prey location can provide a means of drill control in the near future.

DOCUMENTATION OF ANNUAL GROWTH LINES IN THE OCEAN QUAHOG *ARTICA ISLANDICA* LINNÉ

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About 42,000 ocean quahogs (*Artica islandica*) were marked for release at a deep (53-m) oceanic site off Long Island, NY, in 1978. Shells of live specimens recovered 1 and 2 years later have been radially sectioned, polished, and etched for preparation of acetate peels and examination by optical microscopy or microprojection; selected specimens were similarly prepared for examination by scanning electron microscopy. Specific growth-line and growth-increment microstructures are described and photo-illustrated. An annual periodicity of microstructure is documented. The observations form a basis for resource assessment ageing studies of the commercially important species.

THE CHESAPEAKE BAY BLUE CRAB FISHERY: HISTORICAL TRENDS AND EMERGING ISSUES

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Twenty-year trends in the Chesapeake Bay (Virginia and Maryland) blue crab fishery were measured with National Marine Fisheries Service data. Despite a recent downward trend in landings, Virginia continues to have the largest annual harvest of blue crabs in the U.S. While the total number of crabbers in Virginia has been stable, there have been decreasing numbers of users of trotlines and dredges and increases in users of pots. The mean harvest per crabber has fluctuated with a perceptible downward trend; but consistently rising ex-vessel prices have maintained rising gross income in the fishery. Maryland landings, like Virginia's, are a significant portion of U.S. harvest and have shown a slight downward trend. The number of Maryland crabbers has more than tripled over the observed period—predominantly from additions to the recorded number of part-time laborers.

There has not been a decline in the use of trotlines in Maryland, as in Virginia, because of restrictions on the use of pots in certain Maryland waters. In Maryland, the mean harvest per crabber has fallen over the period. Consistently rising ex-vessel prices have resulted in an upward trend in mean labor income for Maryland pot crabbers, but there has been a drop in mean labor income for Maryland trotline crabbers. Based upon this review, three factors affecting the future growth of the industry are discussed: (1) state laws to protect brood stocks differ and confuse stock management efforts; (2) current public management programs (primarily licensing) may not be promoting maximum economic yield from the fishery; and (3) economic uncertainties restrain development of processing facilities and, in turn, discourage harvest.

MANAGEMENT OF THE BLUE CRAB FISHERIES IN NORTH CAROLINA: A CASE HISTORY

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Blue crabs support one of North Carolina's most important fisheries. The recent expansion of the crab fisheries has resulted in numerous management problems concerning resource allocations and gear conflicts. Regulatory authority for management in North Carolina has been delegated by the General Assembly to a 15-member commission which enacts regulations based on staff recommendations and input from the industry and general public. A key management tool is the proclamation authority which has been delegated by the Commission to the Secretary of the Department of Natural Resources and Community Development to respond rapidly to management needs. Proclamations can be issued to invoke a management action with a minimum of 48 h of public notice. This is generally done to open or close areas to a particular fishing method or to set seasons. This ability allows effective response to rapidly changing situations within the fisheries and the stocks. An example of North Carolina's management system involving the blue crab fisheries concerns resource allocation in certain tributaries of Pamlico Sound. Potting and trawling are incompatible gears competing for space and resource. Each is controlled by proclamation. The decision to allow a certain fishery to occur is based on biological, economic, and social implications, with multiple-use resource management and protection being major factors in the decision. Tagging studies are being used to evaluate management strategies and their effect on maximizing crab harvest, and to determine short-term migratory habits. Numerous other management issues affecting blue crabs and their fisheries such as minimum size limit, mandatory cull rings in pots, spawning

sanctuaries, and nursery area protection are addressed.

THE TEXAS OYSTER STUDY. I. RELATIONSHIPS BETWEEN AVAILABLE FOOD, OYSTER COMPOSITION, CONDITION, AND REPRODUCTIVE STATE

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We examined the relationships between what is available for the oyster to eat, the oyster's proximate composition, its condition, and its reproductive state. Changes in the proximate composition of oysters were associated with changes in the annual cycle of fattening, storage, and reproduction. The fattening phase was characterized by high dry-weight condition indices and elevated carbohydrate (glycogen) concentrations. A "storage cycle," the transition from stored glycogen to the lipid reserves in developing eggs, was evident in *Crassostrea virginica* (Gmelin). The gonadal index and percent lipid composition of the oyster were positively correlated. Spawned oysters had low lipid and carbohydrate concentrations, low condition and gonadal indices as well as high concentrations of water and protein. Available food for the oyster was measured as a food index. The food index was defined as the percentage food (food = lipid + carbohydrate + protein) in the total seston. The food index was higher in the spring and summer and was correlated with the gonadal index of oysters. Apparently, the amount of food was greatest at the time of greatest energy demand; that is, during gametogenesis.

THE TEXAS OYSTER STUDY. II. MODELS OF OYSTER NUTRITION IN THE NATURAL ENVIRONMENT

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Two FORTRAN models were developed to integrate information about measured food levels (i.e., the food index) with the presumed needs of the oyster. One model assumed no selective ingestion on the part of the oyster. Another model assumed that the oyster could selectively ingest

organic material. Although the results of the models are in fair agreement with published literature, this agreement could simply be fortuitous. The correspondence between the models we developed and other works, however, suggests the possibility that the food index is a useful measure of available food, that the simplifications made in the models are reasonable ones, and that enough particulate food was present to sustain oysters in the area studied.

A CYTOGENETIC METHOD AS A TOOL FOR ASSESSING THE CONDITION OF SHELLFISH LARVAE

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As a means of assessing their condition at the cellular level, cultured oyster larvae were examined cytologically by employing a relatively simple squash technique. Chromosome groups, and normal and abnormal cells and nuclei were evident. Bacteria also were discernible with this method. These observations were an indication of general health of the larvae in culture and provided some information regarding subsequent development and survival. In addition to being able to observe pathological states of the cells and bacterial infections, one could use the procedure to determine the numbers of cells in mitosis as an indicator of growth rate. Larvae, potentially, could be pre-treated with colchicine to arrest cells in mitosis for counting the chromosomes to obtain karyotypes as an aid in plankton identification. Cytological analyses of the larvae could have many uses in toxicological studies, including bioassays, as well as in hatchery rearing and breeding.

ISOLATION AND PARTIAL CHARACTERIZATION OF A MALATE DEHYDROGENASE FROM *CRASSOSTREA VIRGINICA* (GMELIN)

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Final details of glucose metabolism in marine bivalve molluscs are yet to be elucidated. Malate dehydrogenase (E.C.1.1.1.37) has been implicated in the catabolic pathway leading to the formation of succinate, a major end product of anaerobic metabolism in bivalve molluscs. Further clarification of this metabolic scheme may be gained by an examination of the properties of malate dehydrogenase (MDH). Homogenates of tissues of *Crassostrea virginica* contain at least 3 MDH isoenzymes. One of these was isolated from acetone powders of mantle and gill tissue by ammonium sulfate fractionation, gel permeation, and ion-exchange chromatography. Some properties of this preparation were determined. The Michaelis-Menten constants were: $K_{m(OAA)} = 1.18 \times 10^{-4}$ M; $K_{m(NADH)} = 4.86 \times 10^{-5}$ M; $K_{m(mal)} = 1.35 \times 10^{-3}$ M; $K_{m(NAD)} = 1.30 \times 10^{-4}$ M. The following were not substrates: $NADP^+$, α-ketobutyrate, α-ketovalerate, α-ketoglutarate, D-malate, pyruvate, succinate, oxomalonate. Tartronate, D-, L-, and mesotartrate were not substrates and were found to be competitive inhibitors of malate oxidation. The pH optima were: 7.6 for NADH oxidation and 9.5 for NAD^+ reduction. MDH was inhibited by p-chloromercuribenzoate and N-ethylmaleimide. Listed in decreasing order of effectiveness, Cd^{++}, Zn^{++}, Cu^{++}, Co^{++} and Ni^{++} inhibited NADH oxidation by MDH.

COMPARISON OF THE GROWTH OF *CRASSOSTREA VIRGINICA* (GMELIN) AT FIVE ALGAL RATION LEVELS WITH SPECIFIC REFERENCE TO PREDICTIVE FEEDING EQUATIONS

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Mixtures of the algae *Thalassiosira pseudonana* Hasle et Heimdal (clone 3H) and *Isochrysis* aff. *galbana* Parke (T-ISO) were fed at each of 5 levels to juveniles of *Crassostrea virginica*. The oysters were grown for 3 wk at 25°C and a salinity of 30 ppt. The relationship between algal ration level and oyster growth is presented. The results are discussed with specific reference to several feeding equations either published or in use or both. Recommended algal ration levels are compared for their relative effectiveness. We show that neither cell number, nor volume, nor weight constitute an acceptable parameter for comparing algal species or bivalve species. We recommend that feeding studies be carried out for any new combinations of algae until the nutritive value of the algal species can be correlated with physical characteristics and environmental conditions. The prudent use of predictive algal ration equations as management tools is discussed.

A BLUE CRAB MANAGEMENT PLAN: OBJECTIVES AND RESPONSIBILITIES

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The blue crab, *Callinectes sapidus* Rathbun, of the Atlantic and Gulf coasts supports one of the major marine fisheries of the United States. Regulatory authority

concerning licensing, size and sex limits, quotas, seasons, gear restrictions, and other controls over harvesting within its territorial waters rests with each state, retained by the respective state legislatures, but may be delegated to a commission. Regulations should be based on the best biological, economic, sociological, and environmental knowledge and provide for optimum yield from the resource. The blue crab industry's problems are not limited to regulation of the harvest. They also include the need for federal and state assistance in processing, marketing, and research; conservation of the blue crab habitat; and an adequate data base. A comprehensive blue crab management program should protect the resource, encourage and assist fishing with a minimum of regulations, and promote utilization of the product.

THE BEHAVIORAL BASIS OF LARVAL DISPERSAL AND RECRUITMENT IN THE BLUE CRAB *CALLINECTES SAPIDUS* RATHBUN

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Laboratory experiments have demonstrated that Stage I blue crab zoeae exhibit a number of behavioral traits which should result in distribution high in the water column. These traits include: negative geotaxis which is unaffected by salinity changes of 5 ppt; high barokiness at hydrostatic pressures exceeding 1 atmosphere; increased swimming rate with increased salinity; positive phototaxis at light intensities of $\geq 10^{-3}$ W/m^2; maintenance of swimming speed with decreasing temperature; and the ability to traverse haloclines of 10 ppt as well as sharp thermoclines. Because it is known that female blue crabs migrate to the mouth of Chesapeake Bay to spawn, these behavioral traits should result in massive export of virtually all Stage I zoeae in surface waters. Field evidence by other workers supports this contention. Megalopae possess behavioral traits that differ from late zoeal stages, chiefly, a highly sensitive pressure response, faster swimming speeds, negative geotaxis, and possibly locomotor rhythms that may enhance their transport back into estuaries. Since larval development occurs on the continental shelf, recruitment success of megalopae back into estuaries is likely to be highly dependent on offshore climatological events that determine coastal circulation patterns during the summer and fall.

REPRODUCTIVE PERIODICITY OF *BUSYCON CARICA* (GMELIN) IN WATERS OFF SOUTH CAROLINA

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A total of 1237 knobbed whelks (*Busycon carica*) were collected over a 13-month period near Charleston Harbor, SC. Gonad maturation stages were determined by gonad color and histological sectioning. Monthly fluctuations in gonad weight, penis or nidamental gland weight, gonadal index, and reproductive index were also examined. of the six reproductive characteristics used in this study, gonadal index values were considered to be the best indicators of periodicity. The highest gonadal index values for males occurred in September, October, November 1979, and in March 1980. The highest values for females occurred from September 1979 through May 1980. Sex ratios fluctuated monthly. The number of females was significantly higher than the number of males from July 1979 through January 1980. This situation was reversed in April 1980 when the number of males was significantly higher than the number of females. Sex ratios also fluctuated when examined using shell-length classes. The smallest individuals in the monthly samples were females (60–64 mm). All individuals with shell-length values > 159 mm were female. Sex ratio relationships to reproductive periodicity are discussed.

DISTRIBUTION, SIZE, AND SEX COMPOSITION OF THREE SPECIES OF *CALLINECTES* IN THE COASTAL HABITAT OF THE SOUTH ATLANTIC BIGHT

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Collections by shrimp trawl during summer of 1980 at depth of 4.5–18 m between Cape Fear, NC, and Cape Canaveral, FL, showed that biomass of *Callinectes sapidus* Rathbun was greater than that of the other 72 decapod species collected. *Callinectes similis* Williams ranked fourth in abundance among the other decapod species collected, but *C. sapidus* and *C. ornatus* Ordway were not as numerous. Catches of *Callinectes* spp. were greatest in the nearshore depth zone of 4.5–8.5 m. Density and biomass totaled for all strata were greatest for *C. similis* and *C. ornatus* off Florida, and for *C. sapidus* off South Carolina. Few mature or ovigerous females of *C. similis* and *C. ornatus* were collected, whereas most females of *C. sapidus* were either mature or ovigerous. Significantly more females than males of *C. sapidus* were collected. The ratio of M:F for other *Callinectes* spp. varied with location. Sizes of crabs were not correlated with depth or distance from shore.

NURSERY CULTURE OF THE BAY SCALLOP *ARGOPECTEN IRRADIANS IRRADIANS* (LAMARCK) IN SUSPENDED MESH ENCLOSURES

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Suspended mesh enclosures with bottom areas of 0.1 m^2 were used to grow hatchery-reared bay scallops in Long Island Sound in 1980 and 1981. The enclosures were constructed of 3- or 7-mm polyethylene mesh and were anchored at a depth of 8 m and buoyed with styrofoam floats. Scallops as small as 4.6 mm were successfully grown to a size > 20 mm in the units. Acclimated scallops deployed in the spring of 1981 at temperatures as low as 5 °C survived and subsequently grew normally as water temperatures increased. Scallop densities between 250 and 15,000/m^2 were tested in the enclosures, and although final shell height was inversely related to density, substantial growth occurred at all densities. Biovolumes of up to 3.9 ℓ/enclosure were obtained. Some comparisons between culture of small scallops in mesh enclosures in Long Island Sound and in raceways were made and both systems were useful for nursery culture of this species.

ABSTRACTS OF TECHNICAL PAPERS

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POPULATION STRUCTURE AND PRODUCTION OF THE AMPHIPOD *COROPHIUM SALMONIS* STIMPSON IN GRAYS HARBOR, WASHINGTON

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The tube-dwelling amphipod *Corphium salmonis* is a dominant benthic organism and important food resource in the estuarine mudflats of Grays Harbor, WA. Intertidal core samples were collected at two sites during the spring and summer of 1980 to determine the population structure, biomass, rate of growth, and production of *C. salmonis*. The abundance of *C. salmonis* ranged from 200 to 50,000 individuals per m^2. Peak abundances occurred during July and August. Abundances at the 1.8-m stations were higher than at the 0.6-m stations. Females of *C. salmonis* attained sexual maturity at a length of 4.0–4.5 mm. Brooding of eggs began in April and continued through the end of sampling (30 September). Male-female ratios were lower for sexually mature individuals of *C. salmonis* than for immature individuals, apparently as a result of predation on sexually mature males which wander over the tideflats in search of females. Male-female ratios decreased in the lower intertidal zone, apparently as a result of increasing predation pressure. Ratios also decreased over time at all stations, suggesting that predation pressure may also increase through the spring and summer. An inverse relationship between male-female ratios for mature and immature amphipods suggests a possible genetic response to disparate sex ratios among mature individuals. Data from both natural populations and from cohorts which were artificially isolated inside *in situ* cages were used to obtain size-specific growth rate curves and production estimates for *C. salmonis*. Total *Corophium* production for each station between 1 April and 30 September varied from 3.6 to 10.7 g/m^2 dry wt. *Corophium* production was higher at the upper intertidal stations. Turnover rates (the ratio of production to mean biomass) ranged rom 7.2 to 8.6. The production and turnover rates of *Corophium salmonis* are high relative to other invertebrate species. Thus, this amphipod is an important contributor to secondary production in Pacific Northwest estuaries, providing an important food resource for its predators, many of which are commercially or recreationally valuable. This production must be taken into consideration when making decisions relating to activities such as dredging and filling which have potentially adverse impacts on intertidal areas.

PROGRESS IN THE DEVELOPMENT OF RESISTANCE AGAINST SUMMER MORTALITY THROUGH SELECTIVE BREEDING OF PACIFIC OYSTERS

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Since 1974 the University of Washington's School of Fisheries has been conducting research in the genetics of the giant Pacific oyster *Crassostrea gigas* (Thurnberg). The main emphasis of this work has been the development, through selective breeding, of oyster stocks with high survival potential during summer mortality. Summer mortality is a phenomenon that routinely accounts for losses of from 10 to 60% of harvestable 2-year-old oysters in bays of the states of Washington and California, and Japan. The breeding program began as a selection of individuals from wild populations. The selection process was based upon survival during elevated temperature (21 °C) challenges. The breeding of these individuals (one male mated with one female) produced families of oysters which could be tested and compared on growing grounds experiencing annual mortalities. On the basis of high survival during actual summer mortality, families were selected as the brood lines for future generations. Of 103 families tested since 1977, up to 78 have had higher survival than non-selected controls. The primary goal of the breeding program is to provide brood stock to commercial hatcheries for production of oyster seed resistant to summer mortality. However, for the past three years, the families have also been monitored for growth, gonadal development, and glycogen storage. Since reduced gonadal development and high glycogen content are desirable commercial characteristics, these parameters have also been used in our overall breeding plan. Brood stocks which appear to show promise have been made available to commercial hatcheries since 1978. Data are now being processed and evaluated from the experimental families which will provide valuable information concerning heritability of glycogen levels, and experiments are being conducted on the effects of inbreeding. With every step, an understanding of oyster genetics is clearer and the goal of commercial production of superior oysters is closer.

SURVIVAL AND GROWTH OF THE LARVAE OF *HALIOTIS KAMTSCHATKANA* JONAS AT DIFFERENT TEMPERATURES

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Larvae of the pinto (or threaded) abalone *Haliotis kamtschatkana* were reared at four temperatures, 14, 16, 18.5, and 21°C in 2-ℓ glass beakers. Survival at the end of the experimental period was best at 18.5° and worst at 21°. More rapid settlement observed at higher temperatures may have improved survival at those temperatures by shortening the vulnerable planktonic stage during which most mortalities occurred. Abalone at the highest temperature (21°) showed signs of thermal stress and experienced total mortality. During early embryonic development, from fertilized egg through the trochophore, the lowest temperature (14°) produced the most normal larvae and highest survival. At higher temperatures progressively more mortalities and abnormalities occurred. Larvae reared at 18.5° were consistently of greatest size at settlement; however, abalone reared at 16° grew more rapidly and obtained the greatest length at the end of a 2-month period.

RECENT DEVELOPMENTS IN THE SPOT PRAWN FISHERY IN HOOD CANAL, WASHINGTON

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Hood Canal, a major arm of Puget Sound, is located in northwestern Washington about 48 km (30 mi) west of Seattle. This is the only area in Washington that has consistently produced commercial quantities of the spot prawn *Pandalus platyceros* Brandt. Harvest for both commercial and personal use (recreation) has been restricted to shellfish pot gear since the early 1950's. Increased commercial fishing pressure and poor recruitment between 1972 and 1974 resulted in a decline in spot prawn abundance and serious conflict between commercial and recreational fishermen. This necessitated emergency season closures in 1974, 1975, and 1976. The year 1977 marked the beginning of a new management approach for the Hood Canal spot prawn stocks and associated fisheries. Season lengths and opening dates were set according to the results of a preseason stock assessment and anticipated fishing effort. To ensure an equitable share of the available surplus for recreational fishermen the season was opened first to sport fishing and later to commercial harvest. By 1979, all fishermen were restricted to the use of shellfish pot gear having a mesh size of ≥ 2.2 cm (7/8 in). This was initiated to protect juvenile prawns and to increase total yield. Changes in management appear to be working well. Since 1977, stock abundance has increased from a pre-season index of 1.13 kg (2.5 lb) to 3.06 kg (6.75 lb) per pot in 1982. Harvest is also at an all time high. Nearly 95 metric tons were taken in both 1981

and 1982. Improved fishing success has also, in part, led to a tremendous increase in fishing pressure. The rate of increase has averaged nearly 50% per year since 1977. Better methods of effort-control are now needed to deal with the rapid expansion of this fishery.

POTENTIAL FOR APPLICATION OF THE CHEMICAL DOPA TO COMMERCIAL BIVALVE SETTING SYSTEMS

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Simple chemical compounds have been shown to trigger attachment and metamorphosis of the larvae of several species of marine invertebrates. The simplest molecules in which settlement inducing activity has been demonstrated are L-3, 4-dihydroxyphenylalanine (DOPA), gamma-aminobutyric acid (GABA), and choline. These molecules occur in the marine environment as covalently bounded compounds associated with adhesives, lubricants, exoskeletal proteins, and pigments. A review of numerous studies clearly implicated these chemical cues in successful habitat selection by invertebrate at the termination of the planktonic stage of the life cycle. The similarity between these molecules and neurotransmitters suggests that the chemoreceptors are modified either ontogenetically or phylogenetically from receptors specific to the neurotransmitters dopamine, GABA, and acetylcholine. Selectivity in response by larvae to a given chemical appears to depend on the neurotransmitter-like portion of the compound, whereas specificity appears to depend on the protein, carbohydrate, or lipid constituents. Pediveligers of the blue mussel *Mytilus edulis* Linné and the giant Pacific oyster *Crassostrea gigas* (Thurnberg) settle in response to the amino acid DOPA. Implementing the use of chemicals to commercial setting systems depends on being able to either modify the chemoreceptors so that they respond to an inexpensive and easily available chemical and/or manipulating settlement behaviors. The initial objectives of my study were to determine the response of oyster larvae to DOPA, to examine the potential for application to existing commercial setting systems, and to determine the effect of several environmental factors on the degree of response. Aliquots of hatchery-reared pediveligers of *C. gigas* were tested for attachment in culture dishes to both aged oyster shells and the smooth glass surface of culture dishes. The pediveligers were reared at 34 ppt and at 25°C. Within individual tests, the settlement response by the pediveligers was examined following exposure to DOPA at 0.00001 M while varying the salinity (25 to 35 ppt) and

temperature (20 to 30°C). Controls were run without the addition of DOPA. The results presented are preliminary findings and only indicate observed trends. In tests which offered only a smooth glass surface for settlement, attachment of the larvae to the glass occurred after 24 hr with but not without the addition of DOPA to the seawater. In tests to which DOPA was added the highest percentage of attachment occurred at a salinity/temperature combination of 35 ppt/30°C. The pediveligers also attached to the glass surface at the following salinity/temperature combinations listed in order of decreasing percent response: 35 ppt/25°C, 35 ppt/20°C, and 30 ppt/30°C. After 48 hr, a relatively high number of pediveligers attached to the glass surface in the runs without DOPA at a salinity/temperature combination of 35 ppt/30°C. Also at 35 ppt/30°C in the runs with DOPA a smaller, but significant, percentage of the pediveligers metamorphosed (indicated by new shell growth) without attaching to the glass surface. This did not occur in any of the other runs. The oyster pediveligers were next tested for attachment to aged oyster shells in response to the addition of DOPA. Preliminary results indicate that there was a slightly greater set after 24 hr onto the shells in the tests with DOPA. However, exposure of the larvae to DOPA also promoted attachment to the glass surfaces of the culture dishes. The consequence was that after 48 hr, the set onto the shell was greater in the runs without DOPA, although the total percentage of larvae which undergo metamorphosis appeared to be the same. In the runs with DOPA a significant percentage of the larvae either attached to the glass surface or metamorphosed without attaching to any substrate. These findings suggest that DOPA will not increase the percentage of set onto oyster shells when the setting is allowed to occur over several days. Rather, these findings clearly suggest that the use of DOPA promotes extraneous setting onto otherwise unfavorable substrates. However, these findings do not discount the possibility that chemicals can be used to obtain a more rapid set. The use of chemical cues appeared more applicable to setting systems in which no preferred setting substrate is used, such as in the setting of clams and clutchless oysters.

JAPANESE OYSTER DRILL STUDIES

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The Japanese oyster drill *Ocenebra inornata* (Récluz) is an economically important predator of oysters in areas along the west coast, as well as in its native Japan. Since its accidental introduction into Puget Sound with shipments of Pacific oyster seed, attempts to control this snail have included expensive hand picking and mercuric chloride. These animals aggregate during certain times of the year, and it is suspected that this behavior is cued by water-borne pheromones (chemical substances which enable communication between animals). Pheromones are currently being used in the control of several insects (e.g., gypsy moth) and might have potential as a control technique for the Japanese oyster drill. It was necessary, therefore, to develop an appropriate bioassay to test different water extracts for pheromones. Bioassays consist of subjects (in this case snails), stimuli (water with suspected chemical agents), and responses (which should be easy to identify, associated with the stimuli, reproducible, and rapid). Bioassays should also minimize the water used for stimulus and control to decrease efforts involved in chemical extraction and concentration. Large numbers of snails must be assayed to give statistical credibility to sometimes subjective behavioral data. Several bioassays have been based on the snail's rheotactic response (in a current of water, the snail moves upstream). The Pratt choice chamber was rejected because large volumes of water were needed with only one snail per run. Riffle flumes were rejected because turbulent flows were encountered. Cephalic antennal elongation (after pipetting a small amount of water in front of the snail) was also rejected because of (1) the highly subjective nature of the response (i.e., when are the antennas elongated?), and (2) the large time requirement of (10 min/subject) with the undivided attention of the research. The inadequacies of these bioassays led to work currently being done on a trough bioassay. A test chamber 1 X 1.5 m (39 X 50 in.) was constructed with stimuli and controls (aged sea water) entering the flume through overflowing 1-ℓ beakers. Several hundred snails were placed 1 m from the beakers and the numbers of snails climbing up the beakers during a 6-hr period are noted. Current research using this apparatus includes: (1) dye studies to determine the water depth necessary for good mixing; (2) determination of the threshold flow rate to induce rheotaxis in oyster drills; (3) testing of flow rates with a known stimulus (oyster effluent); and (4) testing of stimuli from whole ground snail extracts and field-filtered effluents from aggregations. Stimuli found to be effective in these bioassays may eventually be used to bait traps or disrupt snail behavior to control Japanese oyster drills on oyster beds.

PROBLEMS ASSOCIATED WITH THE REARING AND SETTING OF LARVAE OF THE CALIFORNIA MUSSEL *MYTILUS CALIFORNIANUS* CONRAD IN A HATCHERY

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Mytilus californianus was successfully spawned and its larvae were reared through metamorphosis in the University of Washington hatchery at Manchester, WA. Although success in spawning and rearing may vary with the hatchery location and methods, data indicated the unreliability of induced spawning at any given time. Some effects resulting from different experimental combinations of temperature and salinity have been observed. Survival of larvae to the pediveliger stage at 18°C and 32 ppt was 31%. The larvae all settled at the lower part of the suspended seed ropes because they have a tendency to sink to the bottom of the tank throughout metamorphosis. Further, higher numbers of the larvae settled when the water was "conditioned" with adult mussels.

A HISTOLOGICAL STUDY OF THE GASTROINTESTINAL TRACT OF THE TANNER CRAB *CHIONOECETES BAIRDI* RATHBUN (DECAPODA, REPTANTIA)

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The tanner crab *Chionoecetes bairdi* is a commercially important species in Alaska about which little is known of its histology. In this study of the tanner crab, the morphology and histology of the gastrointestinal tract is examined and compared to that of the blue crab *Callinectes sapidus* Rathbun. Three histological stains were used: hematoxylin and eosin, periodic acid-Schiff (PAS), and the Feulgen reaction with picro-methyl blue. The foregut, midgut, and hindgut were examined. The fore- and hindguts are both of ectodermal origin, and exhibit similar cuticular layers, epithelial cells, and tegmental glands. The endodermally derived midgut and caeca differ significantly from the fore- and hindgut both in their lack of cuticle, and in the vacuolation of the epithelial cell nuclei. One morphological difference that was noted between the tanner and blue crabs was the absence of aborizations in the posterior midgut caecum of the tanner crab. The function of this caecum may be for osmoregulation. Prolonged osmoregulation in brackish and fresh water occurs to a significant extent in the blue crab but not in the tanner crab because it remains in a marine environment. This difference in habitats may explain the variation in caecum structure. In most other aspects, the histology and morphology of *C. sapidus* closely resembled those of *C. bairdi.*

THE EFFECT OF POPULATION DENSITY ON THE GROWTH OF THE BUTTER CLAM *SAXIDOMUS GIGANTUS*

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Butter (or smooth Washington) clams, *Saxidomus giganteus* (Deshayes), were grown for 2 yr at 4 population densities (96, 48, 24, and 12 clams/0.25 m² plots) in a Latin Squares arrangement at the −0.5-m tide level (MLLW) on a privately owned beach approximately 1 km west of Port Gamble on Hood Canal in Washington State. The clams, dug up from within 10 m of the experimental site, and were individually numbered and measured in length, width, and thickness to the nearest 1 mm and placed into three groups, each containing one third of the naturally occurring population, depending on the clam length. The medium sized group ranged from 76 to 80 mm, with the small and large groups taking the remainder. The plots were filled by randomly selecting from the three groups, with one third of each plot represented by each of the three size groups. The clams were planted in 1978 during the spring tidal series closest to the summer soltice. They were removed, remeasured and replanted at a similar tide in 1979. In 1980, the clams were removed for the last time, during the soltice tidal series. In order to compare the growth differences in the 4 population densities, Walford plots of length at one time versus length at another were made. Walford plots were also made for width and for the product of length and width. The resulting plots showed that there was an appreciable difference in growth between the 48 and 24 clams/plot. The 96 clams/plot had the same growth slope as the 48/plot. The difference between the 12 and 24 clams/plot was also negligible. The data indicated that the maximum density for best growth is 24 clams/0.25 m² (96/m²). The experiment also demonstrated the usefulness of Walford plots to optimize population in a grow-out situation as used in shellfish aquaculture.

THE FEEDING BEHAVIOR OF THE TEREBELLID POLYCHAETE *THELEPUS CRISPUS* JOHNSON IN RESPONSE TO CURRENTS

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The role of currents in determining the feeding behavior of *Thelepus crispus* was investigated as part of a large-scale research project on the response of bottom-dwelling communities to organic enrichment and pollution. Live worms were collected from the intertidal beach at Garrison Bay on San Juan Island, WA. They were placed in natural sediments, in specially designed flow tanks at the Seattle Aquarium and at the University of Washington Friday Harbor Labs. After the worms reconstructed their tubes, the feeding behaviors were observed under three different current velocities ranging from 1 to 8 cm/sec. Particle settlement experiments were also conducted at the three velocities to determine if flow affected the settlement of food around the feeding worms. To clarify any morphological limitations which might affect the choice of food or feeding method in *Thelepus,* the tentacles of preserved specimens were examined under a scanning electron microscope. To corroborate findings in laboratory experiments, field observations and flow measurements were made using SCUBA gear at Garrison Bay, WA. When *Thelepus* is exposed to different current velocities it orients its feeding tentacles in response to the direction of flow and the areas of maximum particle settlements. At speeds < 2 cm/sec, particle settlement is relatively even around the worm mounds and *Thelepus* spreads it tentacles in all directions on the sediment as well as in the water column. It is under this type of flow condition that *Thelepus* is abundant in the field. Suspension feeding may play an important role in food gathering for *Thelepus.* At higher current speeds (4 to 8 cm/sec) particle settlement becomes differentiated between upstream and downstream areas around the worm. The upstream face of the mound has relatively few particles settling out. The downstream face and area immediately behind the worm mound has greater amounts of particles settling out. The placement of tentacles mirrors the settlement patterns of particles. The strength of the current is an important consideration as to how *Thelepus* feeds and where it gathers its food.

VERTICAL MIGRATION OF *GONYAULAX CATENELLA:* POTENTIAL IMPLICATIONS FOR MANAGEMENT OF PARALYTIC SHELLFISH POISONING (PSP) PROBLEMS

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The diel vertical migration pattern of the dinoflagellate *Gonyaulax catenella* Whedon et Kofoid which produces paralytic shellfish poisons, may have important implications for management decisions by industry, public health agencies, and research groups. This migration pattern influences the length of time shellfish at different tide heights or depths below rafts are exposed to *G. catenella.* The exposure should be considered by health agencies, along with tide height or depth, when planning routine sampling and by the shellfish industry when selecting bivalve species to plant or dredging depths. Because the vertical migration pattern is greatly affected by the degree of stratification of the water a predictive model which involves field studies of the effects of changes in density gradients on density of *G. catenella* should be developed. The vertical migration pattern appears to be extremely important in the development of large populations of *G. catenella* in certain sheltered bays, from which significant numbers of *G. catenella* may then be exported to waters outside the bay. An understanding of the functioning of such bays may be useful in determining timing and sites for monitoring and in selection of sites for controlling *G. catenella* with the parasite, *Amoebophrya* (if laboratory tests indicate such control would be safe, desirable, and feasible).

ABALONE AND SCALLOP CULTURE IN PUGET SOUND

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Three new species were cultured at Point Whitney Shellfish Laboratory during 1979–82; the native pinto (or threaded) abalone *Haliotis kamtschatkana* Jonas, the red abalone *Haliotis rufescens* Swainson, and the purple hinge (or giant) rock scallop *Hinnites multirugosus* (Gale). A pilot hatchery system was developed and various culture conditions, methods, and temperatures were investigated. Growth of the pinto abalone was followed over a period of 3 yr in the hatchery. Comparisons of growth and survival rates between juvenile pinto and red abalone were investigated over a one-year period. The pinto growth rate was affected by the type of culture container used and by the presence or absence of light. At one year of age, pinto abalone shells averaged 20 mm. At two years, mean shell length was 37 mm, and the oldest year-class averaged 59 mm at three years of age. Various scallop culture methods, feeding densities and container configurations affected the scallop growth rates. Salinity tolerance was studied and salinities < 23 ppt were detrimental to normal growth and survival. Field plantings at Lopez Island, Port Blakley, Willapa Bay, Manchester, Bellingham Bay, and Point Whitney were studied for growth and survival of juvenile rock scallops. Growth rates of 4.2 mm/mo were achieved at some locations.

PSP: ITS HISTORY, PROCESSES AND IMPACTS AS APPLICABLE TO PUGET SOUND

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This report provides a synopsis of available information concerning the history, processes, and impacts associated with paralytic shellfish poisoning (PSP) in Puget Sound. Paralytic shellfish poisoning is a form of food poisoning in which extremely lethal toxins, produced by certain dinoflagellates, are accumulated in shellfish and passed on to humans. Outbreaks of PSP appear to be spreading to previously unaffected areas. They are increasing in intensity worldwide as well as within the Puget Sound basin. This report includes a review of these trends and of the current toxicity monitoring program established in the state of Washington to protect the public from PSP. Attention is also given to what causes toxic dinoflagellate blooms, particularly dinoflagellate cysts, and contributing environmental factors (i.e., temperature, precipitation, and nutrients). Apparently, numerous environmental factors may influence development of a bloom from newly emergent germlings. In addition, the introduction of certain organic compounds, called chelators, to coastal waters may create an environment favoring growth of the dinoflagellate population by controlling the availability of certain growth-regulating trace metals. A discussion of the nature of dinoflagellate toxins and their possible effects on man and other organisms is included. The recent discovery that dinoflagellate toxins may be lethal to organisms other than man has serious implications: for example, consumption of toxic shellfish may prove fatal to certain species of birds. Additionally, recent investigations indicate that lethal levels of dinoflagellate toxins can be accumulated, retained, and passed up the food chain by herbivorous zooplankton that feed on toxic dinoflagellates.

COMMERCIAL MARICULTURE OF A BAY SCALLOP *ARGOPECTEN CIRCULARIS* (SOWERBY) IN THE ENSENADA OF LA PAZ, BAJA CALIFORNIA SUR, MEXICO

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Mexico's first private shellfish aquaculture company was formed in La Paz, BCS. A local bay scallop, the Pacific calico scallop *Argopecten circularis*, is grown in lantern nets suspended from long lines. Scallop spat are collected by putting sticks of plastic mesh in nylon "onion bags" which are tied five to a weighted line and hung from long lines. Collectors are set out in the spring and the seed scallops are removed 2 to 5 mo later. Significant numbers of scallop spat also regularly set on the lantern nets. Seed scallops are grown in pearl nets during the nursery phase of culture, then grown to market size in lantern nets. Fouling is removed from the nets by a saltwater spray from a gasoline-powered water pump. Scallops are stocked at a density of $25/0.1 \text{ m}^2$ (50 per level) for the final growth stage. Market size (5 to 6 cm) is reached in 5 to 7 mo. Four metric tons of scallops were marketed in Mexico City in the first year of production. A pufferfish, *Spheroides annulatus* (Jenyns), preyed on cultured scallops by chewing open the bottom compartments of some lantern nets. This was alleviated by shortening the lantern nets by 3 levels. A hatchery was constructed, and in the first experiment scallops were conditioned, spawned, and the larvae reared to juvenile stage. Improvements in the grow out system should include using 5-level lantern nets in 2 mesh sizes (12 and 21 mm), and submerging the long lines by 0.5 m. An annual production of 10 tons appears necessary for profitability, with 20 to 30 tons possibly optimum.

PSP RESEARCH: RECENT ADVANCES IN ANALYTICAL AND BIOCHEMICAL STUDIES

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Paralytic shellfish poison (PSP), or "Red Tide," is a persistent problem in the northern coastal areas of the United States and monitoring of shellfish is accomplished via mouse bioassays. We have developed an alternate analytical technique for measuring the toxins using high pressure liquid chromatography. Comparison of both techniques showed high correlation when toxin content in shellfish samples contained about 60 μg toxin per 100 g meat. The mean variation was 25% when higher amounts of toxin were present. Variation in the mouse bioassay is $\pm$ 20%. Preliminary and proposed work will be reported on the biochemical aspects of uptake, storage, and release of the PSP toxins in shellfish.

DISASTER AHEAD FOR THE YAQUINA BAY OYSTER INDUSTRY?

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After 115 years of fishing and farming, the future of Yaquina Bay is as uncertain and bleak as ever, with one exception. The history of this bay, located in Newport, OR, parallels histories of other west coast growing areas. The oyster schooners from San Francisco, the old-time oyster tongers, the replacement of the native Pacific oyster *Ostrea lurida* Carpenter by the giant Pacific oyster *Crassostrea gigas* (Thurnberg), the wood products pollution, the local town's sewage, the infamous tidal wave, and the massive siltation problem are all elements and events of the past 115 years. The current crisis seems to be of major proportions and threatens the future of oyster farming. Generally speaking, oysters are no longer growing to full potential. Kumamoto oysters (variants of *C. gigas*), which were grown on the bottom 15 years ago, now grow only from rafts. Giant Pacific oysters, as of 8 years ago, became stunted after the second year of growth, only putting on thick layers of blistered shells that were filled with a foul-smelling exudate. They seldom reached "medium" size even after 6 years. Perhaps related to this is the fact that several other forms of sea life have almost disappeared from our area over the past 30 years. The source of this problem is unknown, but could be related to the destruction of the ocean food chain over the years. The stunting problem also has been observed in other locations on the west coast. The only ray of hope for this company is to repeat the great switch of the 1920's. That is, change species of oysters once again. The Japanese oyster, *Crassostrea ariakensis* (Wakiya) (= *Ostrea/Crassostrea rivularis*), seems to be the answer. After experimenting for five years, we discovered these advantages: (1) 50% faster growth than *C. gigas*, thereby shortening the growth cycle by one year; (2) good flavor; (3) absence of the stunting and blistering problem; (4) larger maximum size than *C. gigas*; (5) higher spawning temperatures resulting in a firm and tasty meat during August and September; and (6) uniform shell shape and attractive interior shell surface.

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COVER PHOTOMICROGRAPH: *Female specimen of* Alpheus heterochaelis *Say (Decapoda; Alpheidae) collected 26 June 1982 from an oyster reef near Beaufort, North Carolina, USA (scale bar = 5 mm). Photographed with 4 × 5-inch Graphic (Graflex) camera and Xenar lens (# 1: 4.7/1.35) using Kodak Tech Pan 2415 film and processed in HC 110, F-dilution. (Exposure = 5 sec at f 45.) [Photograph provided by Henry E. Page, University of North Carolina, Institute of Marine Science, Morehead City, North Carolina.]*

JOURNAL OF SHELLFISH RESEARCH

SYMBIOTIC ASSOCIATIONS INVOLVING THE SOUTHERN OYSTER DRILL *THAIS HAEMASTOMA FLORIDANA* (CONRAD) AND MACROCRUSTACEANS IN MISSISSIPPI WATERS

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ABSTRACT   The symbiotic relationships between the southern oyster drill *Thais haemastoma floridana* (Conrad) and two species of crabs, the blue crab *Callinectes sapidus* Rathbun and the striped hermit crab *Clibanarius vittatus* (Bosc), were investigated in Mississippi. The crabs provided passive transport and food (attached fouling organisms) for the attached drills; 99 blue crabs carried 203 drills ($\bar{X}$ = 2.0 ± 2.1 drills crab^{-1}, range = 1–17; mode = 1, N = 55 crabs); 233 hermit crabs carried 299 drills ($\bar{X}$ = 1.3 ± 0.8 drills crab^{-1}, range = 1–6; mode = 1, N = 194 crabs). Drills attached to blue crabs were twice the mean height and six times the mean weight of those attached to hermit crabs (36.8 mm and 8.9 g versus 18.5 mm and 1.4 g, respectively). During one survey period 30 of 423 blue crabs (7.1%) and 97 of 1,360 hermit crabs (7.1%) carried drills. The oyster drill/blue crab symbiosis persisted while spawning female crabs congregated around Mississippi's offshore barrier islands during the early fall of 1980 and ceased when the crabs died or migrated to deeper water during late fall. The oyster drill/hermit crab symbiosis was continuous. Drills attached while the crabs were buried at the seawater/substrate interface, resting under peat outcroppings, or while scavenging among grass roots and jetsam. Once mounted, the drills were not readily dislodged by movement of the crabs. In the laboratory drills more readily mounted hermit crabs with attached drills and/or acorn barnacles than hermit crabs without these organisms. A typical mounting took only seconds to complete; drills readily attached to moving hermit crabs. Drills dismounted from hermit crab shells when in the immediate vicinity of live oysters. The drills preyed on acorn barnacles (*Chelonibia patula* [Ranzani], *Balanus* spp.), oysters (*Crassostrea virginica* [Gmelin], *Ostrea equestris* Say), and slipper shells (*Crepidula* spp.) that fouled the blue crab carapaces and hermit crab shells. Two other gastropods (*Cantharus cancellarius* [Conrad] and *Odostomia impressa* [Say]) were occasionally attached to blue and hermit crabs that carried oyster drills.

KEY WORDS   Blue crab, commensalism, macrocrustaceans, oyster drill, phoresis, striped hermit crab, symbiosis

INTRODUCTION

The southern oyster drill *Thais haemastoma floridana* (Conrad) (Gastropoda; Muricidae) is the most destructive predator of the American oyster *Crassostrea virginica* (Gmelin) in coastal Gulf of Mexico waters from Florida to Texas (Burkenroad 1931; St. Amant 1938; Butler 1953, 1954; Gunter 1953, 1979; McConnell 1953; Chapman 1955, 1958; Menzel and Hopkins 1955; Menzel et al. 1957, 1966; Hofstetter 1959; May and Bland 1970; May 1971; Pollard 1973; Breithaupt and Dugas 1979). Mortalities of oysters from drills can be as high as 50% a year (St. Amant 1938). Drills prefer water salinities that usually exceed 18 to 20 ppt (St. Amant 1938, Gunter 1979), and thus oyster reefs located near open Gulf waters are subjected to drill predation during periods of drought or reduced freshwater inputs (from extended closures of water impoundments). Offshore, high salinity areas serve as reservoirs for drills; when inshore salinities increase, the drills invade nearshore reefs as planktonic veliger larvae. The larvae spend about a month in the plankton and are widely dispersed (Butler 1953). After metamorphosis, juvenile drills grow rapidly and can grow an average of 28 mm a year (range = 20 to 42 mm) (Butler 1953).

During the fall of 1980 I observed southern oyster drills attached to many blue crabs (*Callinectes sapidus* Rathbun) and gastropod shells occupied by striped hermit crabs

(*Clibanarius vittatus* [Bosc]) in shallow waters around Mississippi's barrier islands. The drills were being passively transported by the crabs. St. Amant (1938) and Fotheringham (1976) reported this symbiotic relationship, but not to the extent that I observed along Horn and Ship islands. St. Amant found four and five drills attached to two blue crabs in the vicinity of Grand Island, LA. He also noted that drills occurred on flotsam. Fotheringham found juvenile drills on 1.7% of all gastropod shells (> 20 g) that were occupied by *C. vittatus* along the Texas coast. Mark Chatry (Louisiana Dept. Wildl. Fish., St. Amant Marine Laboratory, Grand Isle, LA, pers. comm.) found drills on blue and striped hermit crabs in lower Barataria Bay, LA, in the vicinity of Grand Isle during 1980 and 1981. The late Capt. L. J. Gorenflo of Biloxi, MS, photographed two blue crabs with two and four drills attached, respectively, that were trawled from Biloxi Bay channel in Mississippi Sound in 1953 (photograph provided by W. J. Demoran, Gulf Coast Research Laboratory, Ocean Springs, MS). Capt. Gorenflo noted on the photograph that most of the crabs were alive, but some were weak and dead. His photograph is the only evidence that this drill/crab symbiosis occurred previously in Mississippi waters.

Other muricid oyster drills participate in similar drill/crab symbioses along the Atlantic coast (Table 1). Federighi (1931) reported that the Atlantic oyster drill *Urosalpinx*

cinerea Say utilized hermit crabs as a means of transport in lower Chesapeake Bay. Harold Haskin reported (in Carriker 1955) that on two occasions in Delaware Bay he found five previously marked drills (*U. cinerea*) on shells of the Atlantic moon snail *Polinices duplicatus* Say that were inhabited by the flat-clawed hermit crab *Pagurus pollicaris* Say. Some of the drills were attached to shells of hermit crabs that were no larger than their own shells. One marked drill attached to and was transported 3.5 m by a large hermit crab within 15 minutes of release. Haskin suggested that hermit crabs may play an important role in the distribution of oyster drills. MacKenzie (1962) reported that large numbers of the thick-lipped oyster drill *Eupleura caudata* (Say) and lesser numbers of *U. cinerea* were transported on the carapaces of most horseshoe crabs (*Limulus polyphemus* [Linnaeus]) that he dredged from Long Island Sound. One crab carried 761 thick-lipped and 4 Atlantic oyster drills. He described their symbiotic association as *phoresy*. (Cheng [1973] defined phoresy as a nonparasitic association in which the smaller species, the phoront, is mechanically carried on or in the larger species, the host, and no metabolic interaction or dependency occurs.) Richards Nelson (in Carriker 1955) reported as many as 140 Atlantic oyster drills per horseshoe crab in New Haven Harbor, CT. Fred Sieling (Maryland Dept. Nat. Resour., Annapolis, MD, pers. comm.)

and Michael Castagna (Virginia Inst. Mar. Sci., Wachapreague, VA, pers. comm.) reported that they had occasionally observed blue crabs transporting one or two thick-lipped drills in lower Chincoteague Bay, VA, in the mid-1950's. Federighi (1931) suggested that oyster drills obtained food from fouling organisms attached to the hermit crabs. Others (St. Amant 1938, MacKenzie 1962) found no evidence of drilling on the transport crab. Although several of these authors alluded to a symbiotic association of macrocrustaceans and muricid oyster drills, none attempted to document or quantify the extent of those associations.

This paper describes the nature and extent of the drill/crab symbioses that existed along Mississippi's barrier islands during the fall of 1980. It examines the factors that initiate and control these symbioses which appear to have characteristics of commensalism and phoresis. Hereinafter, I shall refer to the crabs as hosts and to the drills as symbionts. Occassionally, I shall utilize the terms "infestation" and "drill-infested" when presenting and discussing occurrence data and when describing the existence of drills on the shells of hosts. The use of these terms is not intended to infer any parasitic relationship; they are simply utilized in the absence of more appropriate terms. The crustacean and molluscan taxonomies utilized herein follow those of Williams (1965) and Abbott (1974), respectively.

TABLE 1.

A synoptic review of oyster drill/crab symbioses along the Atlantic and Gulf coasts of the United States.

Oyster Drill Species	Crab Species	Locality	Reference
Thais haemastoma haysae[1]	*Callinectes sapidus*	Grand Isle, LA	St. Amant 1938
T. haemastoma	*C. sapidus*	Mississippi Sound, Ocean Springs, MS	(L. J. Gorenflo, 1953 photograph)
T. haemastoma	*C. sapidus* *Clibanarius vittatus*	Lower Barataria Bay, LA	Mark Chatry, LA DW&F, pers. comm. 1981
T. haemastoma	*C. vittatus*	Texas coast	Fotheringham 1976
T. haemastoma floridana	*C. sapidus* *C. vittatus*[2] *Limulus polyphemus*	Horn and East Ship islands, MS	(Present study)
Eupleura caudata	*C. sapidus*	Lower Chincoteague Bay, VA (1956)	Fred Sieling (MD DNR), Mike Castagna (VIMS), pers. comm. 1981
E. caudata	*L. polyphemus*	Long Island Sound, NY	MacKenzie 1962
Urosalpinx cinerea	*L. polyphemus*	Long Island Sound, NY	MacKenzie 1962
U. cinerea	*L. polyphemus*	New Haven Harbor, CT	Richards Nelson (in Carriker 1955)
U. cinerea	"Hermit crabs"	Lower Chesapeake Bay, VA	Federighi 1931
U. cinerea	*Pagurus pollicaris*[3]	Delaware Bay, DE	Harold Haskin (in Carriker 1955)
Calotrophon ostrearum	*Pagurus impressus*[4]	St. Joseph Bay, FL	(E. W. Cake 1981, field observation)

[1] Identified as *Thais floridana haysae*.
[2] Occupying the following gastropod shells: *Busycon contrarium, B. spiratum plagosum, Murex fulvescens, Polinices duplicatus, Strombus alatus,* and *Thais haemastoma floridana*.
[3] Occupying the shells of *P. duplicatus*.
[4] Occupying the shells of *S. alatus*.

MATERIALS AND METHODS

Blue crabs and striped hermit crabs with attached oyster drills were collected at four stations on Horn and Ship islands; those islands form the southern boundary of Mississippi Sound (Figure 1). The crabs were collected in shallow water (< 1 m) with dip nets or crab tongs. On several occasions, all crabs encountered were collected to determine the incidence of infestation. Field observations were made on the behavior of the crabs and drills in their shared habitats. The drills and potential prey items on the crabs' shells (e.g., acorn barnacles, oysters, and slipper shells) were examined for evidence of predation. Infested crabs and their attached drills were placed in individual plastic bags and transported alive in coolers to the Gulf Coast Research Laboratory, Ocean Springs, MS, where they were measured and weighed, and the numbers of drills, barnacles, oysters, and slipper shells per crab (shell) were determined.

In the laboratory, studies of the oyster drill/hermit crab symbiosis were conducted in 70- to 95-ℓ all glass aquaria using sand, seawater, and animals from Horn Island. The experimental crabs occupied the shells of the lightning whelk *Busycon contrarium* Conrad, the pear whelk *B. spiratum plagosum* (Conrad), the southern oyster drill *T. h. floridana*, and the Atlantic moon snail *Polinices duplicatus* (Say), and each was initially infested with acorn barnacles (*Balanus* spp.)

Each trial utilized 5 to 8 crabs, 40 to 50 drills (height range, 15 to 75 mm), and lasted 2.0 to 3.5 hours. Various combinations of crabs (with and without attached barnacles), substrates (sand and oyster shells), oysters (live and empty shells), and in-tank locations of same were utilized during the experiments. Observations were made on the behavior of the drills in relation to the crabs and oysters.

RESULTS

Description of Habitat

Independent drills and crabs and infested crabs shared habitats in the inlets to Horn Island lagoons and in adjacent shallow waters of Mississippi Sound (Figure 1). Those habitats consisted of (1) exposed roots of salt-marsh grasses; (2) submerged grassbeds and root-debris mats; (3) shallow depressions in sandflats and under solid jetsam (e.g., boards and timbers); (4) crevices in and ledges under peat outcroppings; (5) small clumps of oysters; and (6) large groups of oysters attached to submerged structures (e.g., wrecked vessel debris, tree stumps, etc.). The drills and crabs frequently made contact in those habitats, especially when the drills crawled across partially buried blue crabs or quiescent hermit crabs. Drills, crabs, and infested crabs were also trawled-up together from Dog Keys Pass at the west end of Horn Island (Figure 1).
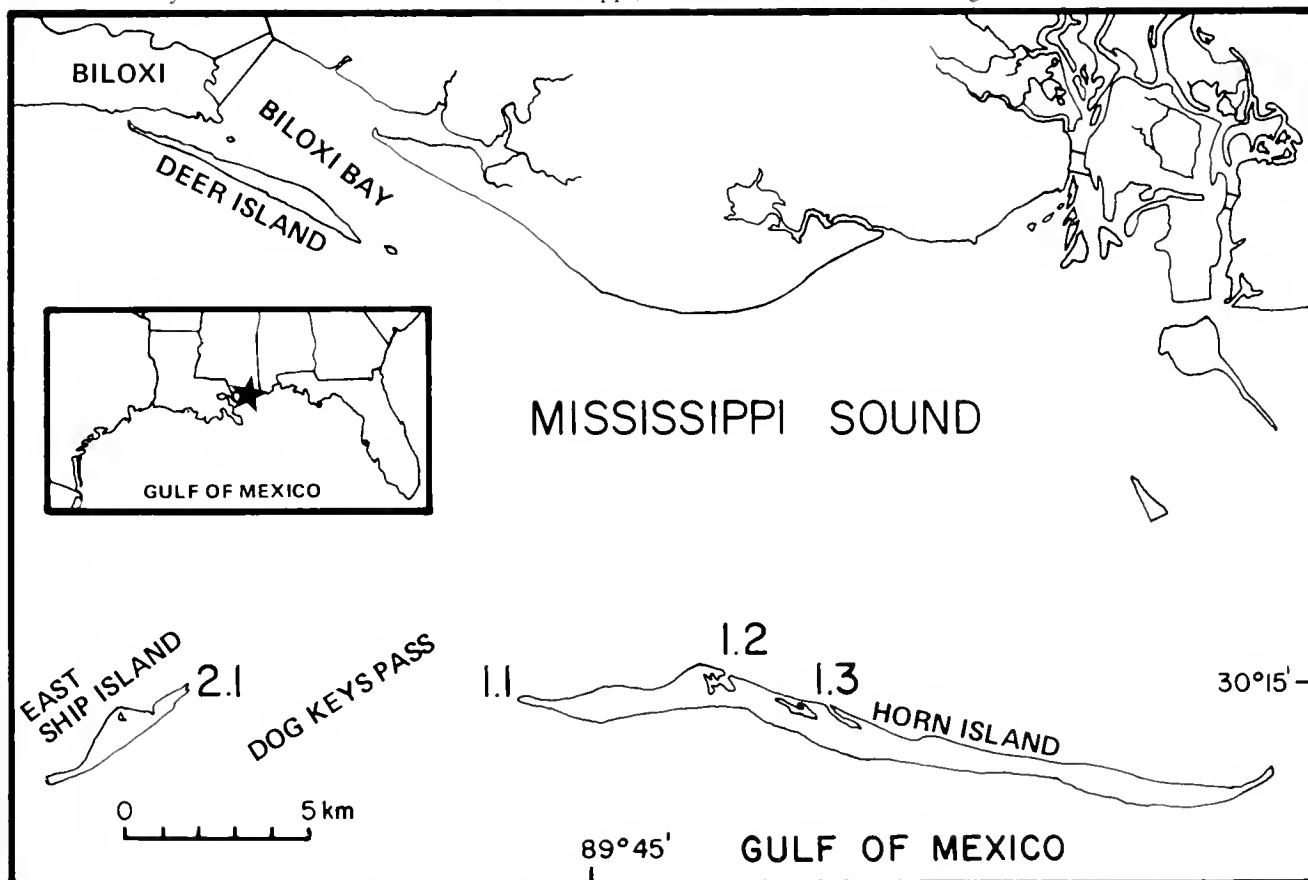
Figure 1. Location of stations where drill-infested blue crabs and striped hermit crabs were collected.

Mean water salinities and temperatures in the study area were 28.4 ppt (24.0 to 30.5 ppt) and 26.1°C (20.0 to 28.0°C), respectively, when drill-infested blue crabs were collected (October 1980), and 21.5 ppt (20.0 to 30.5 ppt) and 19.4°C (18.5 to 27.0°C), respectively, when drill-infested hermit crabs were collected (October and November 1980). Because of visibility and collecting device limitations, all collections were made at depths of 1 m or less. The predominant substrate was well sorted and rounded quartz beach sand, except in the lagoon inlets and along parts of island shorelines where relict peat outcroppings existed.

Oyster Drill/Blue Crab Symbiosis

Ninety-nine infested blue crabs (98 ♀, 1 ♂) were collected from four stations on Horn and East Ship islands on 2, 7, 9, and 14 October 1980. All crabs were adults, while the majority of the drills were juveniles. Mean sizes and weights of the crabs and drills are given in Table 2. The crabs carried a total of 203 drills ($\bar{X}$ = 2.0 ± 2.1 drills crab^{-1}, range = 1−17) (Figure 2); the drills were attached to the carapace (200), the chelae (2), and the abdomen (1). The drill infestation mode was 1 drill crab^{-1} (N = 55 crabs; 55.5% of total); 22 crabs (22.2%) carried 2 drills apiece; 14 (14.1%) carried 3 drills apiece; 2 crabs each (2.2%) carried 5, 6, and 7 drills apiece, respectively; and 1 crab each (1.1%) carried 9 and 17 drills apiece, respectively (Figure 2). No drill-infested blue crabs were observed during three surveys in November (1, 2, and 3 November 1980) and none was seen during numerous surveys during the summer and fall of 1981.

On four occasions at two stations on Horn Island (Stn. 1.2 and 1.3, Figure 1) all blue crabs encountered were collected. Seven percent (30 of 432) of the crabs carried a total of 44 drills (Table 3).

Results of regression analyses of the drill infestation and drill/crab meristic data are presented in Table 4. Only a weak correlation existed between the number of attached drills and the three crab meristics tested (carapace width, weight, and the cross product of the width and weight). In general, however, the larger the crab the larger the number of attached drills.

Other Symbionts on Drill-Infested Blue Crabs

The most abundant epizoan on the drill-infested blue crabs was the symbiotic acorn barnacle *Chelonibia patula* (Ranzani) (see Overstreet 1978, 1982). Each crab carried a mean of 81.8 ± 33.8 (12 to 287) live barnacles on its entire exoskeleton and 35.2 ± 23.7 (2 to 122) live barnacles on its carapace. The numbers of live barnacles on the entire crab and also on the carapace alone were negatively correlated with the number of attached drills (Table 4). Thus, the larger the number of barnacles, the smaller the number of attached drills (i.e., barnacles reduce the space available for attaching drills). Crabs with light barnacle infestations carried 1.4 and 1.7 times as many drills as those with

moderate and heavy infestations, respectively; and crabs with moderate barnacle infestations carried 1.2 times as many drills as those with heavy infestations (Table 5). Thirteen (13.1%) of 99 drill-infested blue crabs had recently dead (empty) barnacles (*C. patula*) on the carapace or abdomen ($\bar{X}$ = 30 barnacles crab^{-1}, range = 1 to 8, N = 39 barnacles). Two oyster drills were observed feeding on barnacles attached to two crabs during the study, but the barnacles did not appear to be an important food source for the drills in general; only 39 of 8,099 (0.5%) barnacles on the 99 drill-infested crabs were dead (empty).

Two (2.2%) of the 99 drill-infested crabs also carried one specimen each of the buccinid gastropod *Cantharus cancellarius* (Conrad), a common omnivore of mud/sand bottoms in high salinity areas of Mississippi Sound. (Five

TABLE 2.

Summary of data from crabs that were infested with oyster drills at four stations on Horn and East Ship islands, Mississippi.

Category	Blue Crabs	Striped Hermit Crabs
Number drill-infested crabs	99	233
Total number drills	203	299
Mean number drills crab^{-1} (Range)	2.0 ± 2.1 (1 - 17)	1.3 ± 0.8 (1 - 6)
Infestation mode (drill crab^{-1})	1 (N = 55)	1 (N = 194)
Percent infested[1]	7.10%	7.13%
Mean size of crab[2] (Range)	152 ± 13 mm (117 - 183 mm)	82 ± 32 mm (23 - 159 mm)
Mean weight of crab[3] (Range)	152 ± 38 g (71 - 269 g)	49.2 ± 27.5 g (3.2 - 120 g)
Mean height of drill (Range)	36.8 ± 11.5 mm (3.0 - 73.8 mm)	18.5 ± 7.6 mm (4.2 - 47.3 mm)
Mean weight of drill (Range)	8.9 ± 9.1 g (0.1 - 53.6 g)	1.4 ± 1.9 g (0.1 - 14.1 g)
Number barnacle-infested crabs	99	103
Total number live barnacles[4]	8,099	896
Mean number barnacles crab^{-1} (Range)	81.8 ± 33.8 (12 - 287)	8.7 ± 18.8 (0 - 120)
Number *Crepidula*-infested crabs	14	106
Total number *Crepidula*	14	603
Mean number *Crepidula* crab^{-1} (Range)	1.0 (1)	5.7 ± 5.7 (0 - 26)

[1] Data from crab subpopulations (see Table 3).
[2] Blue crab (carapace width); hermit crab (gastropod shell height).
[3] Blue crab plus fouling organisms; hermit crab plus gastropod shell plus fouling organisms.
[4] *Chelonibia patula* (on blue crabs); *Balanus* spp. (on hermit crabs).

Figure 2. Female blue crab *(Callinectes sapidus)* with 16 southern oyster drills *(Thais haemastoma floridana)* on carapace and 1 (not visible) on chela. Crab width (carapace) and weight: 150 mm and 151 g, respectively. Mean drill height and weight, (ranges): 31.8 mm (12.8 – 40.3) and 4.8 g (0.3 – 8.4), respectively. Total weight of all drills: 81.6 g. Infested crab was captured at the west end of Horn Island, MS, (Stn. 1.1) on 2 October 1980.

TABLE 3.

Incidence of oyster-drill infestation on crabs collected at four stations on Horn and East Ship islands, Mississippi.

Category	Blue Crabs[1]	Striped Hermit Crabs[2]
Total number crabs	423	1,360
Number infested crabs	30	97
Percent infested	7.10%	7.13%
Number drills	44	119
Mean number drills on infested crabs	1.47	1.23
Mean number drills on all crabs	0.10	0.09

[1] Combined data: Chimney Lagoon, Stn. 1.2 (7 & 14 October 1980) and Ranger Lagoon, Stn. 1.3 (9 & 14 October 1980).

[2] Combined data: Chimney Lagoon, Stn. 1.2 (3 November 1980) and Ranger Lagoon, Stn. 1.3 (2 & 3 November 1980).

other blue crabs in addition to the 99 drill-infested crabs were infested with specimens of *C. cancellarius* only.) Fourteen (14.1%) and three (3.3%) of the 99 drill-infested crabs were also infested with single slipper shells (*Crepidula* spp.) and pyram shells (*Odostomia impressa* [Say]), respectively.

Oyster Drill/Hermit Crab Symbiosis

Two hundred thirty-three drill-infested striped hermit crabs were collected at four stations on Horn and East Ship islands on 2, 7, 9, and 14 October and 1, 2, and 3 November 1980 (Table 2, Figure 3). The hermit crabs occupied the shells of 100 oyster drills (*T. h. floridana*) (42.9%), 70 lightning whelks (*B. contrarium*) (30.0%), 42 moon snails (*P. duplicatus*) (18.0%), 17 pear whelks (*B. s. plagosum*) (7.3%), 2 giant eastern murexes (*Murex fulvescens* Sowerby) (0.9%), and 2 Florida fighting conchs (*Strombus alatus* Gmelin) (0.9%). The hermit crabs carried a total of 299 drills (X = 1.3 ± 0.8 drill shell^{-1}, range = 1–6). The infestation mode was 1 drill crab^{-1} (N = 194 crabs, 83.3% of total); 22 crabs (9.4%) carried 2 drills apiece; 12 crabs (5.2%) carried 3 drills apiece; 3 crabs (1.3%) carried 5 drills apiece; and 1 crab each (0.4%) carried 4 and 6 drills apiece, respectively (Figure 3). Mean sizes and weights of the crabs (including the shell and attached epifauna but excluding the drills) and the drills are given in Table 2. In general, the larger the size of the hermit crab shell, the greater the number of attached drills and the larger the size of the attached drills.

On three occasions at two Horn Island locations (Sta. 1.2 and 1.3, Figure 1) all of the striped hermit crabs encountered were collected. Seven percent (97 of 1,360) of

TABLE 4.

Results of regression analyses on data from drill-infested crabs collected at four stations on
Horn and East Ship islands, Mississippi.

Host Crab Species	Correlations (versus number drills)*	r-Value	F-Value	Regression Equation
Callinectes sapidus	Carapace width	− 0.0346	0.166	Y = 2.8935 − 0.0055X
	Total crab weight	+ 0.0326	0.102	Y = 1.7755 + 0.0018X
	Cross product (width × weight)	+ 0.0176	0.030	Y = 1.9339 + 0.0050X
	Number live barnacles crab^{-1}	− 0.1699	2.883**	Y = 2.6023 − 0.0067X
	Number live barnacles carapace^{-1}	− 0.2508	6.508**	Y = 2.8419 − 0.0225X
Clibanarius vittatus	Maximum crab (shell) dimension	+ 0.1836	8.062**	Y = 0.9212 + 0.0044X
	Weight of crab (+shell) versus weight of individual drills	+ 0.2353	17.409**	Y = 0.5851 + 0.0156X
	Cross product (size × weight)	+ 0.2297	12.871**	Y = 1.0820 + 0.0426X
	Number live barnacles shell^{-1}	+ 0.0160	0.059	Y = 1.2797 + 0.0009X
	Number live *Crepidula* shell^{-1}	+ 0.1373	4.438**	Y = 1.2268 + 0.0218X

*(Unless otherwise indicated.)
**(F-Value significant at the α = 0.05 level.)

TABLE 5.

Summary of oyster drill and barnacle infestation data from 99 blue crabs collected at four stations on
Horn and East Ship islands, Mississippi.

Number Blue Crabs	Number Oyster Drills	Mean Number Drills Crab^{-1} (Range)		Number Live Barnacles	Mean Number Barnacles Crab^{-1} (Range)		Relative Intensity* of Barnacles	Barnacle-to-Drill Ratio
69	156	2.26	(1−17)	4,265	61.81	(12−180)	Light	27.4
27	43	1.59	(1− 3)	3,197	118.40	(37−219)	Moderate	74.5
3	4	1.33	(1− 2)	637	212.33	(156−287)	Heavy	159.6
Totals/Means:								
99	203	2.05	(1−17)	8,099	81.81	(12−287)		39.9

*Light = <25% of carapace covered; moderate = 25 to 50% covered; heavy = >50% covered.

the crabs carried a total of 119 drills (Table 3). The 97 drill-infested crabs occupied 44 shells of the oyster drill *T. h. floridana* (45.4%), 26 shells of the lightning whelk *B. contrarium* (26.8%), 20 shells of the moon snail *P. duplicatus* (20.6%), 6 shells of the pear whelk *B. s. plagosum* (6.2%), and 1 shell of the fighting conch *S. alatus* (1.0%).

Regression analyses were performed on three host categories versus the number and/or weight of attached drills (Table 4). All three correlations were weak but positive. In general, the larger the occupied hermit crab shell, the larger the number and size of the attached drills.

Several noteworthy differences existed between the two drill/crab symbioses (Table 2). Drills that were attached to blue crabs were twice the mean height as those on hermit crabs (36.8 versus 18.5 mm) and consequently, six times the mean weight (8.9 versus 1.4 g). Infested blue crabs carried more drills than hermit crabs ($\overline{X}$ = 2.0 ± 2.1 versus 1.3 ± 0.8 drills crab^{-1}, respectively). The maximum number of drills carried by a blue crab (17) was 2.8 times the maximum number carried by a hermit crab (6). Drill-infested blue crabs carried approximately 9.4 times as

many live acorn barnacles as drill-infested hermit crabs (81.8 versus 8.7 barnacles crab^{-1}, respectively); however, the number of drills on blue crabs was inversely related to the number of barnacles, and the number of drills on hermit crabs was directly related to the number of barnacles (Table 4). Although no additional collections were made, the drill/hermit crab symbiosis continued into the fall of 1981, whereas the drill/blue crab symbiosis was not observed when spawning ceased and the onset of colder water temperatures caused blue crabs to migrate into deeper water (late fall, 1980).

Other Symbionts on Drill-Infested Hermit Crabs

Acorn barnacles (896 of *Balanus* spp.) and slipper shells (603 of *Crepidula* spp.) were the most abundant epifaunal organisms on drill-infested striped hermit crabs (Table 6). The mean numbers (and ranges) of barnacles and slipper shells per hermit crab shell were 8.7 ± 18.8 (1 − 120) and 5.7 ± 5.7 (1 − 26), respectively. Weak but positive correlations existed between the numbers of live barnacles and slipper shells on the hermit crab shells and the number of
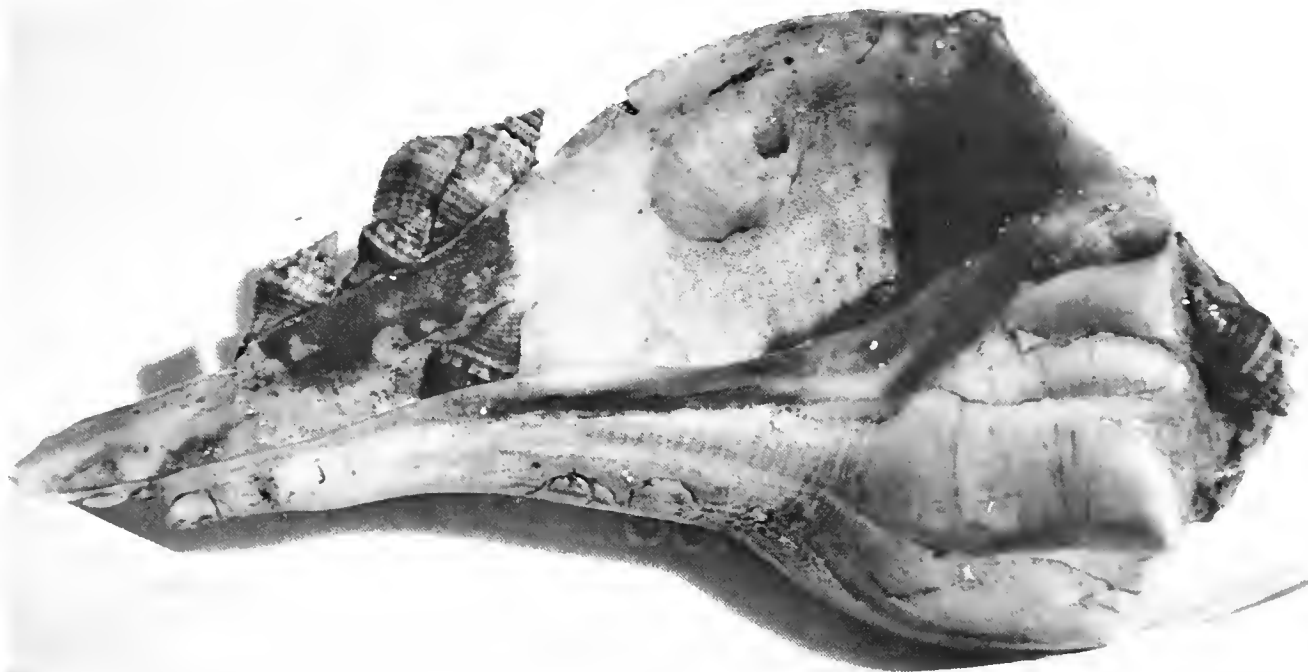
Figure 3. Shell of lightning whelk *(Busycon contrarium)* inhabited by striped hermit crab *(Clibanarius vittatus)* and infested with five southern oyster drills *(Thais haemastoma floridana)* and three spotted slipper shells *(Crepidula maculosa)*. Height and weight of whelk shell (including attached fouling organisms, except drills): 132 mm and 110 g, respectively. Mean drill height and weight, (ranges): 18.1 mm (11.0 − 31.0) and 1.1 g (0.2 − 3.7), respectively. Infested crab was captured in the inlet of Ranger Lagoon (Stn. 1.3), Horn Island, MS, on 2 November 1980.

TABLE 6.

Epifauna of gastropod shells occupied by drill-infested striped hermit crabs at four stations on
Horn and East Ship islands, Mississippi.

Shell Species Occupied	(N)	*Crepidula* spp.	Mean and Range	*Balanus* spp.	Mean and Range	*Ostrea equestris*	Mean and Range
Busycon contrarium	(70)	385	5.5, 1−26	204	2.9, 1− 55	4	0.1, (1)
B. spiratum plagosum	(17)	108	6.4, 2−20	29	1.7, 1− 12	8	0.5, 1−7
Murex fulvescens	(2)	1	0.5, 1	1	0.5, 1	3	1.5, (3)
Polinices duplicatus	(42)	56	1.3, 1− 7	75	1.8, 1− 20	0	
Strombus alatus	(2)	12	6.0, (6)	0		0	
Thais haemastoma floridana	(100)	41	0.4, 1− 5	587	5.9, 1−120	18	0.2, 1−3
Grand totals, means, ranges	(233)	603	2.6, 1−26	896	3.8, 1−120	33*	0.1, 1−7

*9 live; 4 dead with right valve drilled; 20 dead with only left valve remaining.

attached drills (Table 4). In general, the greater the number of slipper shells on a drill-infested hermit crab shell, the larger the number of drills (Table 4). Thus, the presence of attached prey species is directly related to the attractiveness of the crab's shell to foraging drills. The positive correlation in the case of barnacles on hermit crab shells (as opposed to the negative correlation in the case of barnacles on blue crab carapaces) is a function of the total shell space available for foraging drills to attach. (Blue crabs heavily infested with *C. patula* have limited space on the carapace for drills to attach.)

Several oyster drills were observed feeding on epifauna attached to hermit crab shells. One 34-mm drill had rasped a hole and was feeding on a 32-mm oyster spat (*C. virginica*) which was attached to the outside of a 107-mm lightning whelk shell when the host hermit crab was collected. Another 36-mm drill was rasping a hole along the margin of a 29-mm slipper shell (*Crepidula plana* Say) which was attached inside the aperature of a 122-mm lightning whelk shell when the host hermit crab was collected. Only 9 (27.3%) of 33 crested oysters (*Ostrea equestris* Say) found on drill-infested shells occupied by hermit crabs were alive; 4 shells were empty and drilled by a muricid gastropod (probably *T. h. floridana*); and 20 were represented only by their attached left valves.

Additional Drill/Crab Symbioses

During the study, several additional examples of oyster drill/crab symbioses were observed in the vicinity of Horn Island, MS. Several large horseshoe crabs (*L. polyphemus*) along the island's beach had one or two moderate-to-large oyster drills attached to their abdomens. Two additional drill-infested crab species were collected in commercial blue crab traps in deeper water (> 3 m) off the island's north beach. One stone crab (*Menippe mercenaria* [Say]; 95 mm, 184 g) carried five drills (66 to 71 m) and five live barnacles (*C. patula*) on its carapace. One spider crab (*Libinia dubia* H. Milne Edwards; 73 mm, 148 g) carried one drill (62 mm, 34 g) and 85 live and 10 dead barnacles (*C. patula*) on its carapace. Those symbiotic associations may have been artificially produced, however, because the crabs were confined in a trap that attracted and permitted the entry of large numbers of oyster drills.

An additional oyster drill/hermit crab symbiosis was observed during the summer of 1981 in St. Joseph Bay, FL. Four red hermit crabs (*Pagurus impressus* [Benedict]) occupying shells of the Florida fighting conch (*S. alatus*) carried six mauve-mouth oyster drills (*Calotrophon ostrearum*

[Conrad]) (Figure 4). The mean height of the conch shells was 86 mm (78 – 94 mm) and the mean weight of the shell plus crab was 76 g (52 – 93 g). The mean height and weight of the drills were 21.0 mm (17.5 – 23.6 mm) and 1.0 g (0.5 – 1.6 g), respectively. The conch shells were also occupied by five crested oysters (*O. equestris*), one of which was incompletely drilled, and numerous slipper shells (*Crepidula maculosa* Conrad and *C. plana*) of various sizes.

Behavior of Oyster Drills and Hermit Crabs

When given the opportunity to interact with hermit crabs in laboratory aquaria, the oyster drills behaved as follows:

1. The drills more frequently mounted hermit crab shells that had live barnacles attached, and also those that had other drills attached. When live barnacles were present, 179 (91.8%) of 195 drills mounted hermit crab shells; 124 drills (63.6%) attached if other drills were already attached to the hermit crab shells; and 55 drills (28.2%) attached when no other drills were present. When no live barnacles were present on the hermit crab shells, 11 drills (5.6%) attached in the presence of other drills and 5 drills (2.6%) attached in the absence of other drills.

Figure 4. Shell of fighting conch *(Strombus alatus)* inhabited by red hermit crab *(Pagurus impressus)* and infested with two mauve-mouth oyster drills *(Calotrophon ostrearum)* and one spotted slipper shell *(Crepidula maculosa)*. Height and weight of conch shell (including fouling organisms, except drills): 94 mm and 93 g, respectively. Drill heights and weights: 21.4 and 23.6 mm, 1.2 and 1.6 g, respectively. Slipper shell length and weight: 27.0 mm and 2.0 g, respectively. Infested crab was captured in the vicinity of Presnell's Fish Camp, St. Joseph Bay, Port St. Joe, FL, on 15 June 1981.

2. The usual drill-to-crab mounting occurred in the following manner: When the hermit crab shell was encountered, the drill raised its tentacles and siphon, extended them forward, and examined the shell; the drill then raised the forward portion of its foot, attached to the shell, and when most of the foot was connected, it pulled its body and shell onto the host's shell. Once mounted, the drill usually moved around the shell for a few minutes before becoming quiescent. The drill-to-shell mounts were relatively fast and were completed approximately 5 seconds after initial contact.

3. Most drills mounted the part of the hermit crab's shell that was initially encountered, regardless of the position and activity of the host crab's tentacles, eyes, and chelipeds. Drills were able to mount hermit crab shells that were moving when encountered.

4. Drills mounted hermit crab shells from sand and solid substrates with relative ease; 61% of the mountings were from sand and 39% were from aquarium sides, other crab shells, dead oyster shells, and pieces of brick. Drills also attached to passing crab shells while upside-down (shell aperature up) in the sand.

5. On three occasions 15 drills mounted one hermit crab shell (6 drills per hermit crab shell was the greatest infestation observed in the field). Fifteen drills mounted one crab within 50 minutes (0.3 drill min^{-1}). The greatest attachment rate on one hermit crab shell was 11 drills within 6 minutes (1.8 drills min^{-1}).

6. Apparently, oyster drills were attracted to barnacles on the hermit crab shells and remained on the shell until more preferred prey such as oysters were encountered or until dislodged for other reasons. The drills dismounted from hermit crab shells onto or immediately adjacent to live oysters, but rarely remounted the crab shells once on live oysters. Twenty-four (57.1%) of 42 drills in three experiments were transported to live oysters by hermit crabs.

DISCUSSION

Factors Controlling Oyster Drill/Crab Symbioses

Southern oyster drills were attracted to and mounted blue crabs and striped hermit crabs for at least one of the following reasons:

1. *Foraging and the presence of potential food.*

The presence or probable presence of acceptable prey species of the southern oyster drill appeared to be the most important controlling factor in the drill/crab symbioses. St. Amant (1938) and Butler (1953, 1954) reported that drills, especially young ones, will consume barnacles, and that drills of all sizes will prey on oysters and mussels. During this study I observed direct and indirect evidence of drill predation on epifauna of blue crab and hermit crab shells. Direct evidence included actual feeding of drills

on barnacles (on blue crabs) and indirect evidence included *Thais* drill holes in dead oysters and in-progress drilling of a slipper shell (on hermit crab). This is the first known evidence of slipper shell predation by the southern oyster drill. All drill-infested blue crabs had live barnacles attached to their exoskeletons, but if the crab's carapace was heavily infested ($>$ 50% coverage) with barnacles, space availability appeared to limit the number of attached drills. The numbers of barnacles and slipper shells on drill-infested hermit crabs were, however, positively correlated with the number of attached drills.

Foraging drills are negatively geotactic; they will move upward when placed under water, unless they encounter acceptable food in which case they remain with the food species "indefinitely" (Butler 1979). The act of crawling up onto any solid substrate including crab shells or aquarium walls is a normal foraging behavior of oyster drills. Butler (1979) reported that the South Australian drill *Thais orbita* (Gmelin) moved up the walls of a container in the absence of barnacles, but remained with and fed on barnacles (*Balanus glandula* Darwin) when present. Whether the drill's negative geotaxis was automatic or in response to the release of metabolites by potential prey species was not determined and, in the case of relatively small substrates like crab shells, the two behaviors may be inseparable. In the case of these drill/crab symbioses, most initial attachments probably resulted from foraging, but were enhanced if acceptable prey species were present.

2. *The presence of other attached drills (gregarious factor).*

Southern oyster drills are normally gregarious, especially during feeding and spawning when food by-products and pheromones, respectively, are released (St. Amant 1938, Gunter 1979). The presence of 16 drills on the carapace of one blue crab is an example of gregariousness (Figure 2). The 16 drills were clumped together; however, only five live barnacles were present and no feeding or spawning activities were in progress. Thus, some other factor attracted and held the drills on the crab's carapace. During the laboratory experiments, only 11 (5.6%) of 195 drills attached to crabs which had other attached drills but no live prey (barnacles). Thus, this appears to be a minor factor. When the initial field collections were made, the drill spawning season had ended and no reproductive activities were observed among the young drills used in the laboratory behavior trials.

3. *The availability of solid, stable substrates for protection or shelter.*

Oyster drills, especially recently settled juveniles, are normally associated with and attached to firm substrates such as oyster shells, rocks, and submerged objects (timbers, stumps, etc.) for food (epifauna), protection (from predators), and shelter (from currents, waves, and potential

loss of attachment and subsequent abrasion, burial, or predation). Because of the dearth of such substrates in the vicinity of the barrier islands, the attachment of young drills to the crab shells may have been a defensive as well as a foraging behavior. Small drills which were attached to crab shells had a lower probability of being consumed by fish and crab predators than unattached drills. Although striped hermit crabs will kill oyster drills (Gunter 1979), they are unlikely to leave the protection of their gastropod shell to attack attached drills; however, small drills within the aperature of the hermit crab shell may be subjected to such predation. Blue crabs will remove attached drills if they are within reach of the chelae and the crabs can dislodge attached drills by "rubbing" them against aquarium walls. In either case, protection is lost, and the drills may be subject to predation.

4. *The presence of eggs on ovigerous blue crabs.*

Eggs or their by-products which are released from ovigerous crabs may biochemically attract foraging drills. Sixty-four (65.3%) of the 98 drill-infested females were ovigerous, 26 (26.5%) were "spent" (the zoeae had recently hatched), and the remaining 8 (8.2%) had not yet spawned. The probability of drill infestation is greater when the females are ovigerous than when they are not. Of 55 females infested with a single drill, 31 (56.4%) were ovigerous; 16 (72.7%) of 22 females with two drills were ovigerous; 11 (78.6%) of 14 females with three drills were ovigerous; and 6 (75.0%) of 8 females with five or more drills were ovigerous. In a related study of drill damage to blue crabs in commercial traps north of Horn Island, I observed several drills feeding on the "sponge" of ovigerous females. The highly protrusile proboscis of oyster drills permits them to rasp and feed on crab eggs while attached to the carapace and abdomen of ovigerous females.

5. *The presence of biochemical stimulants or by-products from wounded or moribund blue crabs.*

Wounded, moribund, or dead crabs, especially blue crabs, may represent a potential food source for the otherwise carnivorous drills. On several occasions in November 1980, when large numbers of spawned-out females were dead or dying, a few were stranded on the beach at low tide with drills still attached to their carapaces. Were the drills waiting for passive transportation to continue or were they waiting for a meal? During a related study of drill damage to commercially trapped blue crabs north of Horn Island in the spring of 1981, I observed that drills penetrated the crabs' exoskeletons via wound holes, autotomized appendage stumps, thin appendage joints, and occasionally via holes drilled in the carapace. The drills also used their protrusile proboscis to penetrate the thin membranes at the bases of the gills within the branchial chambers to gain access to thoracic muscle tissues. No such crab predation was observed during the present study of 203 drills that were attached to 99 live blue crabs.

6. *Increased random attachment to available substrates by an exploding drill population.*

Environmental conditions near the barrier islands may have promoted the drill/crab symbioses. Extended drought conditions during 1979–1981 increased salinities in Mississippi Sound and permitted the settlement of relatively large numbers of young drills in normally marginal habitats. Those drills became abundant in habitats containing barnacles, mussels, and oysters around the barrier islands. The sheer abundance of the drills and their random attachment to all firm objects may account for their presence on crabs. In those instances when infestation prevalence was determined, blue crabs and hermit crabs exhibited the same prevalence (7.1%). Although I made no attempt to document the presence of drills on flotsam and jetsam around the barrier islands, Federighi (1931) and L. A. Stauber (in Carriker 1955) reported that young oyster drills (*U. cinerea*) were distributed by attaching to floating algae as well as to other flotsam and jetsam. I routinely observed drills on submerged planks and other discarded items in barrier island lagoons during this study.

7. *In response to a programmed symbiotic phenomenon.*
If the drill/crab symbioses are as well established as shown by this and other studies (Table 1), then muricid drills may be programmed to seek crabs for their transportation potential. The availability of transportation to unpopulated areas, especially those with abundant food supplies, may foster the symbiotic relationship.

Probable Role of Macrocrustaceans in the Migration of Southern Oyster Drills

Along the Gulf of Mexico coast, blue crabs and striped hermit crabs are common inhabitants of estuaries and oyster reefs (McDonald 1940, Galtsoff 1964, McClellan 1965, Fotheringham 1976, Bahr and Lanier 1981) where they tolerate a wide range of water salinities and temperatures (Christmas and Langley 1973). Blue crabs move about extensively (Darnell 1959) and can travel as much as 1.6 to 2.0 km day^{-1} (H. Perry, Gulf Coast Research Laboratory, Ocean Springs, MS, and M. Oesterling, Virginia Institute of Marine Science, Gloucester Point, VA, unpublished data). Thus, they could carry oyster drills from barrier island habitats to inshore oyster reefs within a week. In contrast, striped hermit crabs travel much less and usually remain within the littoral and shallow, sublittoral zones (Fotheringham 1975). They travel as much as 156 m day^{-1} (Hazlett 1981) and, thus, could carry oyster drills (to nearby oyster reef) but not as far as blue crabs. On the other hand, oyster drills do not migrate (Butler 1953); unless carried by crabs or other means, the drills probably remain within the vicinity where they originally settled.

In Mississippi Sound, at least three species of crabs (blue, striped hermit, and horseshoe) were observed transporting drills during this study. Thus, the drill/crab symbioses may be important in distributing juvenile and young adult drills. The quantity of drills transported by this means is small when compared with the number of larval drills that are distributed in the plankton to high salinity areas following reproduction. Nevertheless, the crabs might carry drills to areas where currents do not carry larval drills, and they can transport drills throughout the year.

Along the Atlantic and Gulf coasts of the United States, at least four species of muricid oyster drills (*Calotrophon ostrearum*, *Eupleura caudata*, *Thais haemastoma floridana*, and *Urosalpinx cinerea*) and five species of arthropods (*Callinectes sapidus*, *Clibanarius vittatus*, *Pagurus impressus*, *Pagurus pollicaris*, and *Limulus polyphemus*) (Table 1) participate in drill/crab symbioses. Although relatively few reports about these symbioses appear in the literature, I suspect that they are common and have an important role in extending the distributions of oyster drills. MacKenzie (1962) concluded that horseshoe crabs (*L. polyphemus*) were important distributors of Atlantic coast oyster drills (*E. caudata* and *U. cinerea*) throughout Long Island Sound and perhaps beyond. Harold Haskin (in Carriker 1955) concluded that hermit crabs (*P. pollicaris*) played an important role in the distribution and migration of Atlantic oyster drills (*U. cinerea*) in Delaware Bay.

The distributory effects of these drill/crab symbioses may be somewhat negated, however, because blue crabs and striped hermit crabs prey on small oyster drills. Blue crabs in Horn Island lagoons (pers. observ.) and in nearby Lake Pontchartrain, LA (Darnell 1958), readily consume small gastropods which they ingest whole. Gunter (1979) reported that striped hermit crabs killed southern oyster drills in Apalachicola Bay, FL, by pinching their tentacles until they bled to death; thereafter, the crabs pulled the drills from their shells, consumed the flesh and occupied the newly emptied shell. Of 1,360 striped hermit crabs collected during November 1980, from the Horn Island lagoons (Stn. 1.2 and 1.3), 825 (60.7%) occupied shells of the southern oyster drill. (The next most frequently occupied shell was that of the moon snail *P. duplicatus* [23.0%].) Rudloe (1971) documented the attack of a striped hermit crab on a live pear whelk *Busycon spiratum* (Lamarck) in which the crab killed the whelk with its chelae, extracted and consumed the flesh, and occupied the new shell briefly before returning to its "old" shell.

Drill/Crab Symbioses: Commensalism or Phoresis?

Cheng (1967) discussed the importance of commensalism and phoresis in the marine environment and pointed out that the two symbioses differed primarily with regard to nutritional aspects. He defined "commensalism" as a more or less intimate relationship in which the commensal (in this case the drill) generally derives physical shelter from the host (the crab), is nourished on food organisms that are associated with but not a part of the host (barnacles, oysters, slipper shells), and is not metabolically dependent on the host. Literally, commensalism means "eating at the same table." It is a loose type of nonobligatory relationship (Cheng 1967). He defined "phoresis" as a loose, nonobligatory relationship in which one species, the host (crab), merely provides shelter, support, or transport for the other species, the phoront (drill). Metabolic dependency is not involved. In a more restrictive definition, Cheng (1973) considered phoresis as an association in which the smaller of the two species, the phoront, is mechanically carried in or on the larger species, the host, and no metabolic interaction or dependency occurs. It does not involve a sharing of food as does commensalism. According to Cheng's definitions of phoresis, those animals, commonly referred to as being epizootic or epizoic, are engaged in phoretic associations with their hosts.

The symbiotic relationships between southern oyster drills and crabs in Mississippi Sound share components of commensalism and phoresis. The two symbioses can overlap according to Cheng (1967), and this is apparently the case with the drill/crab associations described herein. In a limited sense, the drills derive passive transport (cf., phoresis), shelter (cf., phoresis and commensalism), albeit negligible, and support (cf., phoresis) from the crab hosts. The drills derive nutritional benefit in a nonobligatory fashion (cf., commensalism) from the epifauna on the crab hosts, but the drills do not "share" those prey species in the traditional sense (cf., commensalism) such as do hermit crabs and attached sea anemones. On the other hand, if drills consume eggs from ovigerous blue crab females or attack and kill free-living blue crabs, then the relationship can be considered predatory.

If food availability and utilization are the primary controlling factors in the drill/crab symbioses, the relationships should be categorized as modified forms of commensalism. On the other hand, if, as MacKenzie (1962) observed, the drills primarily derive passive transport from the crabs, the relationships should be categorized as modified forms of phoresis. Cheng (1967) noted a considerable overlapping between commensalism and phoresis, yet he provided no examples of symbioses that shared characteristics of both. He suggested that one type of symbiosis may evolve into another. In that case, neither the commensalitic nor phoretic behavior of the two symbionts appears to be dominating. I suggest, therefore, that the commensalistic components probably evolved first and the phoretic components occurred secondarily. The drill/crab symbioses in Mississippi waters appear to be primarily commensalistic and secondarily phoretic, and perhaps should be defined as phoretic commensalism. Of the seven controlling factors discussed at the beginning of this section, foraging and the presence of attached prey species (on blue and hermit crab shells)

and egg masses (on ovigerous blue crabs) probably initiated the relationships; food availability. gregariousness, and substrate stability (protection and/or shelter) probably prolonged them; and the foraging for new food sources or dislodgment probably terminated the relationships. The drill's "predatory" behavior toward wounded or moribund blue crabs appeared to be an expression of the drill's normal opportunistic feeding, especially when it occurred in commercial crab traps. The possibilities of random attachment to solid substrates and "programmed" transportation attempts appeared to be the least plausible controlling factors.

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PREDATION ON AMERICAN OYSTERS *(CRASSOSTREA VIRGINICA* [GMELIN])
BY AMERICAN LOBSTERS *(HOMARUS AMERICANUS* MILNE-EDWARDS),
ROCK CRABS *(CANCER IRRORATUS* SAY), AND
MUD CRABS *(NEOPANOPE SAYI* [SMITH])

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ABSTRACT Predation on the American oyster *Crassostrea virginica* (Gmelin) by the American lobster *Homarus americanus* Milne-Edwards, the rock crab *Cancer irroratus* Say, and the mud crab *Neopanope sayi* (Smith) was studied in the laboratory. When provided with a range of oysters from 10 to 35 mm shell length (SL), lobsters (55–98 mm carapace length [CL]) and rock crabs (32–107 mm carapace width [CW]) could all open oysters of 25 to 30 mm SL, but they usually selected smaller oysters. Oysters of 30 to 35 mm SL appeared to be a critical size as they were rarely preyed upon by either lobsters or rock crabs. Although all lobsters had a similar broad preference for oysters of 10 to 25 mm SL, larger rock crabs preferred larger oysters than smaller rock crabs. Predation rates were variable among individuals but were generally faster in larger than in smaller lobsters and rock crabs. Maximum mean lobster and rock crab predation rates were 28.0 and 4.5 oysters $\cdot$ predator^{-1} $\cdot$ day^{-1}, respectively. Groups of rock crabs (32–58 mm CW) and mud crabs (14–23 mm CW) that fed on oysters of 2 to 9 mm SL which were attached to spat collectors, averaged 0.59 and 0.44 oyster $\cdot$ crab^{-1} $\cdot$ day^{-1}, respectively. Larger rock crabs (50–76 mm CW), foraging on spat collectors, consumed 1.26 oysters $\cdot$ crab^{-1} $\cdot$ day^{-1}. No discernible sexual differences existed in either oyster size selection or predation rates for the lobsters and crabs. Patterns of oyster destruction were predator-specific. Lobsters opened oysters by indiscriminate crushing, whereas rock crabs exploited weak spots around the shell margin and thin areas in the cup valve. Isolating oyster < 30 to 35 mm SL from decapod predators and barring rock crabs and mud crabs from spat collectors would reduce oyster mortality.

KEY WORDS: Oysters, *Crassostrea virginica*, lobsters, crabs, predation, selectivity, mariculture

INTRODUCTION

The American oyster *Crassostrea virginica* (Gmelin) is cultivated extensively on the eastern coast of North America and has economic importance in many communities. Studies of oysters have identified cancrid, portunid, and xanthid crabs (Menzel and Hopkins 1955, McDermott 1960, Krantz and Chamberlin 1978, MacKenzie 1981), oyster drills (Galtsoff 1964), and starfish (Galtsoff 1964) as the principle predators. (See MacKenzie [1981] for a comprehensive review of oyster mortality factors.)

We found in our laboratory study that American lobsters (*Homarus americanus* Milne-Edwards) are also predators of oysters. Previously it was shown that lobsters prey on several types of molluscs and other invertebrates (Ennis 1973, Elner and Jamieson 1979, Elner 1980, Scarratt 1980). The rock crab *Cancer irroratus* Say preys on oysters in Caraquet Bay, New Brunswick, Canada (R. W. Elner, unpublished data), and on other molluscs and invertebrates in other areas (Scarratt and Lowe 1972, Elner and Jamieson 1979, Elner 1980). The only previous quantitative investigation of oyster predation by rock crabs (MacKenzie 1981)

did not consider opening techniques or size-specific predation rates.

In Caraquet Bay, NB, culturists collect oyster spat on "chinese-hat" collectors, so-called because of the conical collector plates. the 0.33-m diameter plates are stacked in bundles of 12 with a gap of 30 mm between adjacent plates. The bundles are suspended, from rafts or fences, 0.3 m above the sea bottom. Culturists detach oyster spat from the collectors at a shell length of about 23–25 mm and use various protective rearing techniques to grow the oysters to seed. The oysters are exposed to lobsters and rock crabs when relaid as seed onto growing areas at shell lengths from 25 to 60 mm.

We conducted a laboratory investigation on the shell-opening behavior and feeding rates of lobsters and rock crabs on unattached oysters from Caraquet Bay. Predation by rock crabs and mud crabs (*Neopanope sayi* [Smith]) on oysters attached to chinese-hat collectors was also considered. Both crabs are abundant on the collectors suspended in the bay and cause oyster mortality. We were particularly interested in obtaining information about the predators that could be used to improve culture strategy and ultimately increase oyster yields.

MATERIALS AND METHODS

Lobsters and large rock crabs were captured by otter trawl in Passamaquoddy Bay, New Brunswick, Canada, near the mouth of the Bay of Fundy. Small rock crabs, mud crabs, and oysters were collected from commercial oyster beds in Caraquet Bay, NB. The oysters had been grown on the cement substrate which coats the chinese-hat collectors, and thus had cement cultch bonded in their left (cupped) shell valves. During experiments, the predators and oysters were kept in 0.35- × 0.5-m glass aquaria filled to a depth of 0.25 m with running seawater. The seawater temperature was 13 ± 1°C and the salinity range was 29 to 32 ppt throughout our investigations.

Lobster size was measured as carapace length (CL) from the posterior edge of an eye socket to the posterior edge of the carapace, parallel to the longitudinal axis. The sizes of rock crabs and mud crabs were determined by measuring carapace width (CW) between the tips of the distal marginal teeth. Maximum shell dimension ("length") (SL) was measured to express oyster size. All measurements are accurate to the nearest 0.1 mm.

Predators were held without food for 2 days before feeding experiments to standardize hunger levels. Only uninjured, apparently healthy predators and oysters were used.

Predation techniques used by lobsters from 55 to 98 mm CL and rock crabs from 32 to 107 mm CW on oysters of 5 to 35 mm SL were observed. We also observed the techniques used by small rock crabs (32–58 mm CW) and mud crabs (14–23 mm CW) as they fed on oyster spat (2–9 mm SL) which were attached to the chinese-hat spat collectors. Shell fragments were collected to help interpret and describe breaking techniques.

Individual lobsters and rock crabs from three and four size groups, respectively, each group comprising six predators, were presented with five size classes of oysters of ten individuals each. The oysters were spread over the bottom of the aquaria. Prey and predators sizes were:

Oysters (mm, SL): 10–15, 15–20, 20–25, 25–30, 30–35.
Lobsters (mm, CL):   55–63 (♀), 58–62 (♂), 85–98 (♀).
Rock crabs (mm, CW): 32–46 (♀), 35–45 (♂), 73–79 (♂), 94–107 (♂).

The sizes of the predators were within the size ranges that occur on oyster beds in Caraquet Bay. The predators were segregated by sex to determine whether feeding behavior or rates were different. The number of oysters eaten in each size class was monitored daily for 11 days; all oysters eaten were replaced by live oysters of the same size class to maintain prey availability.

Four groups of five female rock crabs and two groups of five male rock crabs (32–58 mm CW) plus two groups of five female mud crabs and four groups of five male mud crabs (14–23 mm CW) were each presented with approximately 200 oysters (2–9 mm SL) which were attached to sections from chinese-hat spat collectors. The crabs were obtained from collectors in Caraquet Bay. In addition, six individual male and four individual female rock crabs (50–76 mm CW) were each provided with a section of a chinese-hat collector which held approximately 200 oysters (2–9 mm SL). After 7 days the number of oyster spat eaten by each predator group was estimated by counting the scars on the collector resulting from successful acts of predation. Individual rock crabs were left 17 days before the number of oyster spat eaten was estimated.

RESULTS

Lobsters and rock crabs appeared to encounter oysters randomly. They would then manipulate them with their mouthparts and anterior walking legs, and finally attempt to crush them.

Lobsters broke small oysters (< 10 mm SL) outright with their mouthparts or crusher chelae, whereas they broke oysters of 10–35 mm SL with their crusher chelae alone. The lobster's slender cutter chela grasped the oyster while the more robust crusher compressed opposite valves of the shell. If the shell did not break, its position was repeatedly adjusted and further compression forces were applied until a weak spot was found and breaking occurred. No one part of the oyster shell appeared to be broken more frequently, as evidenced by the varied shapes of the shell fragments resulting from the lobster's actions (Figure 1A). Oysters that could not be broken after several crushing attempts were usually rejected.

Rock crabs readily crushed small oysters up to 10 mm SL; they held the oyster with one chela and crushed it with the other. Rock crabs appeared more specific than lobsters in opening oysters of > 10 mm SL, although they showed a similar propensity to "test" oysters for weak spots until the shell ultimately broke or was rejected. The most common approach was to chip pieces from the shell margin until a hole was made into which the tips of the chelae could be inserted; then, the shell valves were pried apart. No part of the shell margin appeared to be attacked preferentially. Occasionally, shell valves were not separated and a hole or large gap was made at the edge of the shell. Oysters of up to about 25 mm SL were also opened by making a hole in the central area of the cup valve where the shell was thin. Patterns of damage to oyster shells produced by rock crabs are shown in Figure 1B.

The two crab species exhibited different behaviors when foraging for oysters on collectors. Rock crabs broke oysters while they were attached or detached the oysters before opening them. Mud crabs were restricted to breaking attached oysters.

No observable sexual differences existed in oyster-opening behavior for lobsters or crabs. Once the oyster had been opened, lobsters used only their mouthparts to glean flesh from the prey, while rock crabs used their chelae and mouthparts to tear away the flesh from the broken shell.
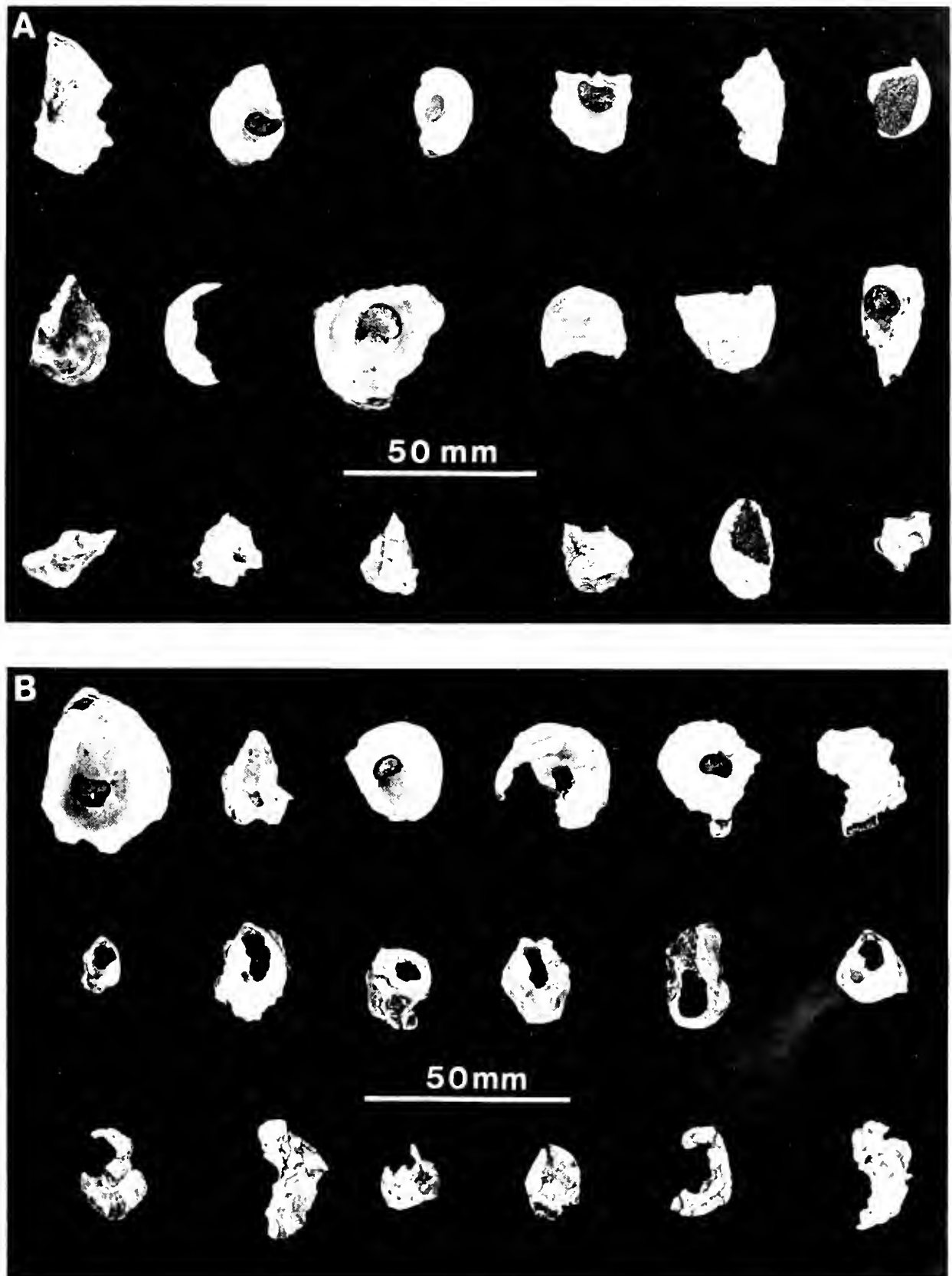
Figure 1. (A) Oyster shell fragments resulting from lobster predation; note the varied shapes of the fragments. (B) Shell fragments from oysters opened by rock crabs; note the characteristic damage to shell margins and central areas of cup valves.

Figure 2 shows that, for all the lobster size groups, predation rates were highest within the small-to-intermediate sizes of oysters (10–25 mm SL) and declined rapidly with larger oysters. Rock crabs also fed on a broad size range of oysters, but larger rock crabs preferred larger oysters than the smaller rock crabs. Oysters of 30–35 mm SL appeared to be at a critical size as they were rarely preyed upon by either lobsters or rock crabs. Feeding rates were variable among predators of the same size group and for individual lobsters and rock crabs from day to day; however, mean daily predation rates increased significantly (P < 0.01) as predator sizes increased for lobsters and rock crabs (Figure 3). Thus, maximum mean rates (± standard error of the mean, SE) by lobsters and rock crabs, 28.0 ± 0.33 and 4.5 ± 1.40 oysters · predator^{-1} · day^{-1}, respectively, were attained by some of the larger predators of each species (Figure 3). The larger rock crabs attained predation rates equivalent to those of the smaller lobsters.

The mean predation rate (± SE) on attached oysters (2–9 mm SL) by rock crabs (32–58 mm CW) in groups was 0.59 ± 0.07 oyster · crab^{-1} · day^{-1}, whereas the mean rate for isolated rock crabs (50–76 mm CW) on attached oysters was 1.26 ± 0.25 oysters · crab^{-1} · day^{-1}. Mud crabs (14–23 mm CW) in groups consumed 0.44 ± 0.09 oyster · crab^{-1} · day^{-1} (Table 1). In contrast to the relationship in Figure 3, there was no correlation (P > 0.05) between predation rate and predator size for isolated rock crabs feeding on attached oysters; however, the relatively larger rock crabs held in isolation had a higher overall mean predation rate on attached oysters than the smaller rock crabs in groups (Table 1).

No discernable sexual differences existed in prey size selection or predation rate for the lobsters and crabs in any of the experimental series. The shape of the diet curves (Figure 2) for male lobsters (58–62 mm CL) and rock crabs (35–45 mm CW) resembled those for similar sized female conspecifics (lobsters, 55–63 mm CL; rock crabs, 32–46 mm CW). Similarly in Figure 3, no significant differences existed in mean predation rates between the similar sized male and female lobsters (♂, 6.93 ± 1.96 and ♀, 6.22 ± 2.57 oysters · lobster^{-1} · day^{-1}; t = 0.23, df = 9, P > 0.5) or the similar sized male and female rock crabs (♂, 0.98 ± 0.11 and ♀, 1.47 ± 0.18 oysters · crab^{-1} · day^{-1}; t = 2.01, df = 10, P > 0.05). Differences in mean predation rates for male and female crabs feeding on attached oysters were not significant (Table 1).

DISCUSSION

Patterns of destruction of oyster of > 10 mm SL were specific for lobsters and rock crabs; therefore, it should be possible to identify the predators on oyster beds by examining oyster-shell fragments. Opening techniques resembling those observed in our study have also been noted by Elner and Jamieson (1979) for lobsters and rock crabs feeding on Atlantic deep-sea scallops, *Placopecten*
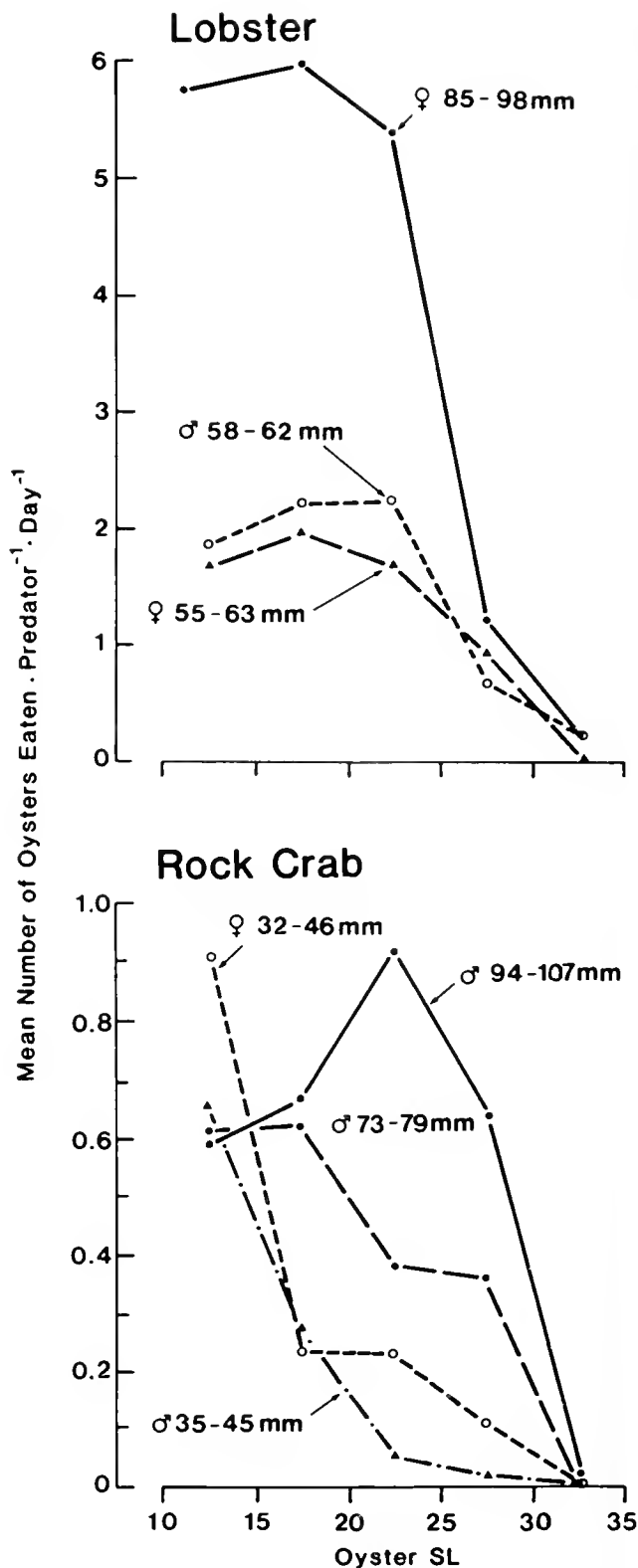
Figure 2. Mean daily oyster consumption per predator plotted against oyster shell length (SL) for lobster carapace length (CL) and rock crab carapace width (CW) size groups.
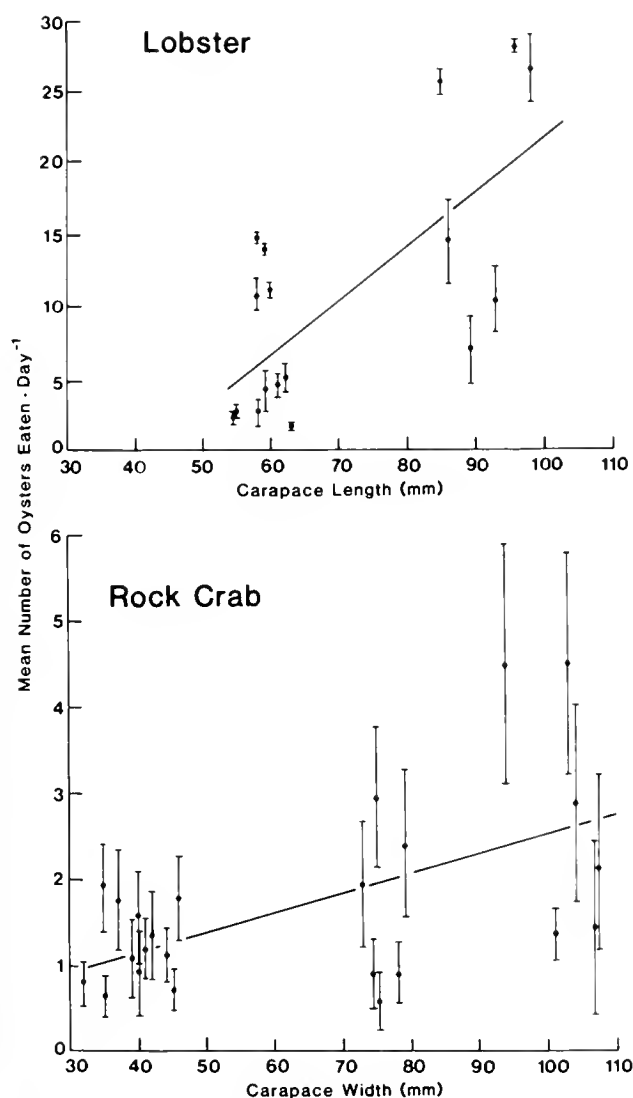
Figure 3. Individual lobster and rock crab predation rates over the entire range of oyster sizes eaten, expressed as mean number ($\pm$ SE) of oysters eaten per day (Y-axis) relative to predator size (X-axis). (The regressions are: lobsters, Y = -15.41 + 0.37 X, R^2 = 0.48; rock crabs, Y = 0.35 + 0.02 X, R^2 = 0.29.)

TABLE 1.

Predation rates of rock crabs and mud crabs on oysters (2–9 mm SL) on chinese-hat spat collectors.

Crab (mm CW)	Sex	Number of Oysters Eaten *over 7 days †over 17 days	Mean Number oysters · crab^{-1} · day^{-1}
Rock Crabs in Groups*			
34, 40, 50, 50, 58	♂	17	0.49
34, 38, 41, 43, 45	♂	24	0.69
32, 39, 46, 47, 51	♀	12	0.34
38, 40, 40, 41, 44	♀	19	0.54
37, 39, 41, 46, 51	♀	22	0.63
32, 41, 42, 43, 54	♀	30	0.86

Mean daily predation rate ($\pm$ SE) = 0.59 $\pm$ 0.10 (♂); 0.59 $\pm$ 0.11 (♀)
(t = 0.02, df = 4, P > 0.5)
Overall mean daily predation rate ($\pm$ SE) = 0.59 $\pm$ 0.07

Isolated Rock Crabs†			
50	♂	19	1.12
58	♂	21	1.24
59	♂	26	1.53
60	♂	12	0.71
74	♂	4	0.24
76	♂	22	1.29
52	♀	27	1.59
52	♀	53	3.12
66	♀	23	1.35
72	♀	7	0.41

Mean daily predation rate ($\pm$ SE) = 1.02 $\pm$ 0.19 (♂); 1.62 $\pm$ 0.56 (♀)
(t = 1.16, df = 8, P > 0.1)
Overall mean daily predation rate ($\pm$ SE) = 1.26 $\pm$ 0.25

Mud Crabs in Groups*			
14, 18, 19, 20, 21	♂	10	0.29
17, 18, 19, 19, 23	♂	14	0.40
18, 18, 19, 20, 21	♂	17	0.49
16, 20, 23, 23, 23	♂	27	0.77
14, 14, 14, 15, 16	♀	6	0.17
16, 16, 17, 19, 19	♀	19	0.54

Mean daily predation rate ($\pm$ SE) = 0.49 $\pm$ 0.10 (♂), 0.36 $\pm$ 0.19 (♀)
(t = 1.28, df = 4, P > 0.1)
Overall mean daily predation rate ($\pm$ SE) = 0.44 $\pm$ 0.09

magellanicus (Gmelin). Krantz and Chamberlin (1978) described six distinct patterns of damage to cultchless oyster spat by the blue crab *Callinectes sapidus* Rathbun; three of the destruction patterns (crushed shells of small oysters, chipped shell margins, and broken spat attachment points) were the same as those observed for the rock crabs.

Our experiments showed that, notwithstanding predator size and the proportionately smaller chelae of the rock crab, both lobsters and rock crabs were able to feed over the same size range of oysters. Mud crabs, also, appeared to be effective predators for their size and were able to open attached oysters of 2–9 mm SL at a similar rate to larger rock crabs. Overlaps in lobster and rock crab predation on

deep-sea scallops and green sea urchins (*Strongylocentrotus droebachiensis* O. F. Müller) have been documented previously (Elner and Jamieson 1979, Elner 1980). Thus, these predators would compete for prey whenever they occur together.

Considering our experimental design, where oysters of all sizes were available, the largest oysters eaten were probably below the absolute maximum size of oyster that predators could open, if small oysters were unavailable. We believe, however, that our upper limit of 30–35 mm SL is a realistic representation of the largest oyster size eaten in the field where alternative prey are always present. All lobsters and rock crabs tested were capable of opening

oysters of 25–30 mm SL, yet they exhibited preferences for oysters in the 10- to 25-mm SL size range (Figure 2). The behavior pattern of predators showing preference for prey of less than the maximum size they can consume has also been observed in the green crab *Carcinus maenas* (Linneaus) (Elner and Hughes 1978, Hughes and Elner 1979, Elner and Raffaelli 1980). Size selection of prey has been reported by Elner and Jamieson (1979) and Elner (1980) for lobsters and rock crabs preying on deep-sea scallops and green sea urchins. Such selection behavior can result from the predator making an active behavioral choice based on prey value, or a passive, mechanical consequence of prey availability and the predator having a set "persistence time" proportional to its hunger level (see Hughes [1980] for review). Our observations suggest that prey size selection is probably a passive, mechanical process. Lobsters and crabs attempted to prey on all oysters they encountered but the larger predators were clumsy in handling small oysters and all predators rejected oysters if they could not break them after a series of force applications. Thus, size-selective mechanisms tended to shift predation pressure away from the small (less easily handled) and large (stronger) oysters and toward the preferred size of oysters. Both the active behavioral and mechanical paradigms for size selection predict that the diet curves should shift to the right as the size of the predator increases (Hughes 1980). Although this relationship was demonstrated for the rock crab, it was not for the lobster.

Predictions of the impact of a predator on an oyster stock based only on prey-selection behavior and predation rates observed in the laboratory are not particularly meaningful. Data on abundance and size frequencies of predators and prey, as well as other factors influencing prey selection and predation rate, are required before a realistic estimate of predation mortality can be made. We believe, however, that the small rock crabs and mud crabs, which are extremely abundant on the oyster beds and spat collectors, kill many more oysters than the more rapacious, but much less common, lobsters and large rock crabs. Similarly, Whetstone and Eversole (1978, 1981) have suggested that *Panopeus herbstii* Milne-Edwards, a mud crab similar to *Neopanope sayi*, is as important as larger crab species as a predator of seed of the northern quahog clam *Mercenaria mercenaria* (Linné) because of its relatively higher abundance and predatory capability. Our laboratory results support the field observations by MacKenzie (1980) that rock crabs and mud crabs cause substantial oyster mortality and show that the decapods tested are capable of consuming large numbers of oysters, and thus have the potential to reduce oyster production. Furthermore, the results show that the 30- to 35-mm SL of oysters is a critical size at which oysters may be virtually invulnerable to decapod predators.

Culturists growing oysters where crabs and lobsters occur should adjust their strategy to protect oyster seed until it reaches 30–35 mm SL. Because small crabs can prey on oyster spat on collectors, culturists should ensure that the collectors are protected from invasion by these crabs.

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STUDIES OF SHELL DISEASE OF THE EUROPEAN FLAT OYSTER
OSTREA EDULIS LINNÉ IN NOVA SCOTIA

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ABSTRACT Shell disease was found in the progeny of the European flat oyster *Ostrea edulis* Linné imported several years ago to Nova Scotia. This disease probably accounted for fibrosis in several tissues of affected oysters, but, in general, had no serious effect on oyster stocks in Nova Scotia. The marine fungus *Ostracoblabe implexa* Bornet et Flahalut was isolated and cultured from infected shells. Electron microscopy of the organism revealed the fine structure of the ovoid enlargements and their morphogenesis under prolonged incubation at 5°C.

KEY WORDS Oyster, *Ostrea edulis*, marine fungus, *Ostracoblabe implexa*, shell disease, oyster pathology.

INTRODUCTION

Shell disease of European flat oysters has been known for many years, and the general symptoms of this disease have been described in detail (Korringa 1951, Alderman and Jones 1971b). The causative agent, however, was not established until the isolation of *Ostracoblabe implexa* by Alderman and Jones (1971a, b). The first indication of shell disease is the development of white spots inside the shell. As the invasion of the shell continues with the penetration of the growing mycelium, more spots appear which coalesce to form white cloudy areas. The perforation of the shell by the infestation appears to cause a change in the secretions of the mantle of the host animal. The extent of conchyolin deposition depends to great extent on the focal intensity of the fungal attack within the shell. At the center of the infestation the conchyolin tends to be in the form of a wartlike excrescence which may be 2 to 4 mm in thickness. In severe cases the excrescences become enlarged, coalescing into one or more knobs in the muscle base. Eventually the area of muscle attachment may become a raised boss. This bosslike excrescence is not found outside the muscle attachment area and typifies the disease called *maladie du pied* in France.

The disease was reported in Britain, France, and the Netherlands (Sinderman and Rosenfield 1967, Sprague 1971, Alderman 1976). It was first observed in Nova Scotia in 1975 in experimental stocks of oysters transferred from Ellerslie, Prince Edward Island. The stocks resulted from the introduction of Dutch stocks from Milford, CT, which were bred in quarantine. A later examination of preserved shells showed that both the parent stock and the first Canadian generation showed symptoms of shell infestation. The presumptive involvement of *O. implexa* was confirmed by D. J. Alderman (Fish Disease Laboratory, Weymouth,

Dorset, England; personal communication) from examination of fresh and preserved shell material and by culture.

A study of the prevalence of the disease was carried out by the Nova Scotia Department of Fisheries in conjunction with Dalhousie University, and the Fish Disease and Nutrition Section of Fisheries and Environmental Sciences, Department of Fisheries and Oceans, in the summer of 1980. The disease appeared to exist in European flat oysters held at Whitehead Harbour and Spanish Ship Bay. This report describes the lesions found in the infected oyster shells, histopathological changes in the oyster tissues, growth and isolation of *O. implexa*, and fine structure of the isolated organism.

MATERIALS AND METHODS

Oysters

Hatchery-produced progeny of imported European flat oysters *O. edulis* were grown on natural beds in Nova Scotia. The 1975- to 1979-year classes of the oyster were sampled from Whitehead Harbour or Spanish Ship Bay of Nova Scotia in May–October of 1980. After gross examination of the specimens for typical lesions of shell disease infection (Alderman and Jones 1971b), the shells were cleaned thoroughly and rinsed repeatedly with sterile seawater, then incubated in sterile seawater at 15°C. Some of the shells were decalcified with an EDTA solution (Alderman and Jones 1971b) or Cal-Ex® (Fisher Scientific Co., Ltd.) for examination by phase contrast microscopy to detect the infective agent(s) within the shell material.

Histology

For histopathological examinations tissues from 20 oysters were fixed in Davidson's fluid (Shaw and Battle

1957) embedded in paraffin, sectioned, and stained with Harris' hemotoxylin and eosin. Photomicrographs were prepared with a Zeiss photomicroscope.

Growth and Isolation of the Infective Agent

Fragments of shell with shell disease lesions were incubated in autoclaved seawater at 15°C for 3 to 4 weeks. The growth of fungal colonies was examined periodically. A pure culture of the organism was obtained by incubation of a small piece of diseased shell in a yeast/peptone medium (Alderman and Jones 1971a, b) at 15°C. Identification of the organism was based on morphology described by Alderman and Jones (1971b) and Alderman (1976, 1980).

Electron Microscopy

The isolated organism was harvested from yeast/peptone medium by low speed centrifugation. The resulting pellets were fixed in 2% glutaraldehyde in phosphate buffer (0.1 M, pH 7.0), postfixed in osmium tetroxide, and embedded in TAAB® resin (Marivac Ltd., 1872 Garden Street, Halifax, NS B3H 3R6, Canada). The ultrathin sections were stained with uranyl acetate and lead citrate (Dawes 1971) and examined using an Hitachi HS-9 electron microscope.

RESULTS

Figure 1A shows white spots coalescing to form a cloudy area on an infested shell. A lesion involving wart formation through deposition of conchyolin by the oyster mantle is shown in Figure 1B. Figure 1C shows a heavily infested specimen with a large sheet of conchyolin embedded in a cloudy area of shell. Examination of several groups of

oysters indicated that the overall prevalence of this disease was approximately 10% (Table 1).

Most of the infestations were in the early stage of lesion development; < 1% of the infested oysters had reached the advanced, heavy warting stage. The prevalence was slightly higher in the older oysters than in the younger ones (Table 1); however, no seriously damaging effect of this disease on the oyster stocks was observed.

TABLE 1.

Percentage occurrence of shell disease among 3- and 5-year-old oysters during May survey (mixture of oysters from Spanish Ship Bay and Whitehead Harbour) and July survey (oysters from Spanish Ship Bay).

Age	Progress of Disease (Stages)*				Total Number
	0	1	2	3	
3 years	1,836 (92.3%)†	132 (6.6%)	11 (0.6%)	11 (0.6%)	1,990
5 years	750 (88.0%)	91 (10.7%)	4 (0.5%)	7 (0.8%)	852
Total No. of oysters	2,586	223	15	18	2,842
Mean % in each class	91.0%	7.9%	0.5%	0.6%	
5 years	94	6	2	1	103
Mean % in each class	91.3%	5.8%	1.9%	1.0%	

*Stage 0 = no disease; stage 1 = one or more white spots; stage 2 = slight warting; stage 3 = heavy warting.
†Percentages in parentheses indicate percentage occurrence of shell disease for oysters in designated year class (i.e., 3 or 5 years old).
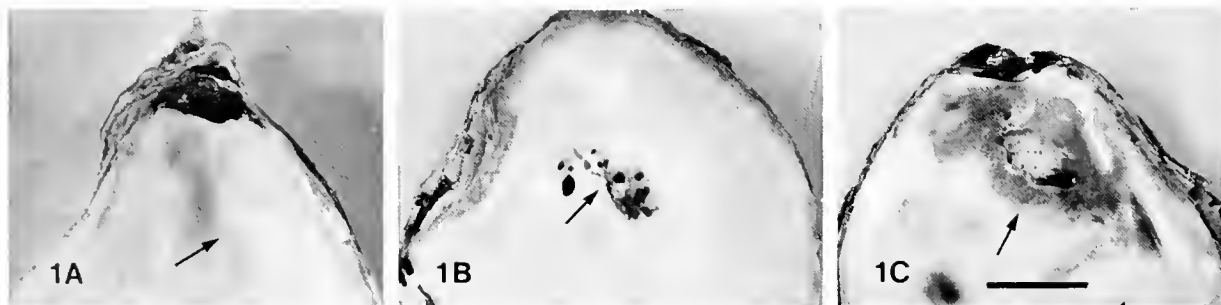
Figure 1. Typical shell disease lesions at various stages: 1A, white spots or cloud (←); 1B, black or brownish conchyolin at center of the warts (←);1C, large sheet of conchyolin deposited in cloudy area (←). Bar = 20 mm

In the tissues of 20 infested oysters examined for the causative agent and possible histopathological changes, no sign of an infective agent was found. Generally there was no apparent ill effect caused by the infestation; however, development of fibrous tissue was evident in the gill, mantle, and digestive tracts of many of the specimens examined (Figures 2A and 2B). Fungal mycelia were easily observed in the decalcified specimens using phase contrast microscopy. Formation of fungal colonies on shell fragments was usually observed after a 3- to 4-week incubation of infested material in sterile seawater at 15°C (Figure 3). Isolation of a pure culture of a fungus was achieved by incubating wart tissue in yeast/peptone medium at 15°C. Figure 4A shows the mycelia of the isolated fungus which exhibited ovoid swelling at frequent, irregular intervals (Alderman and Jones 1971b; Alderman 1976, 1980). The incidence and size of the ovoid swellings appeared to increase with incubation at low temperature (5°C) for an extended period of time; some of the swellings appeared as spherical bodies (Figure 4B). Figure 5 shows typical *O. implexa* in a decalcified specimen that had been incubated for 14 days at 15°C following autoclaving in seawater and inoculation with the isolated organism.

Electron micrographs of the isolated organism are shown in Figures 6 and 7. The mycelium contains vacuoles and various electron-dense bodies. The organelles, such as nucleus, mitochondria, and endoplasmic reticulum, appeared to be well developed in the ovoid swellings (Figure 6A–6D). When the cultures were incubated at 5°C for a prolonged period, proliferation of the endoplasmic reticulum was observed, and the formation of a multilayered heavy wall often resulted (Figures 7A and 7B).

DISCUSSION

The shell lesions of infested oysters found in Nova Scotia were typical of the shell disease described in the literature (Alderman and Jones 1971b; Alderman 1976, 1980). The stocks sampled at Whitehead Harbour and Spanish Ship Bay were produced in the Pleasant Point Hatchery, where the spat and brood stocks were held in the same tank during the first summer at an elevated temperature. The possibility that the parent stocks carried the organism and served as a disease source cannot be ruled out.

Alderman and Jones (1971b) observed an increase in long epithelial cells in mantle tissue of certain heavily infested specimens. The fibrous tissue noted in infested oysters could be a result of the shell disease infestation because an increase in fibrous tissue formation in shellfish appears to be a common and nonspecific reaction to infestation or inflammation of the host animal (Pauley 1969, Sparks et al. 1969, Sparks and Fontaine 1973). The infestation by *O. implexa* did not, however, appear to have any serious physiological effect on the host animal, since most specimens had well developed gonads and some were spawning. Alderman (1980) suggested that levels of shell disease infestation are high only where the water temperature exceeds 22°C for at least 2 weeks. The ambient water temperature in Nova Scotia is generally too cold and, therefore, precludes serious shell disease problems in oyster stocks.
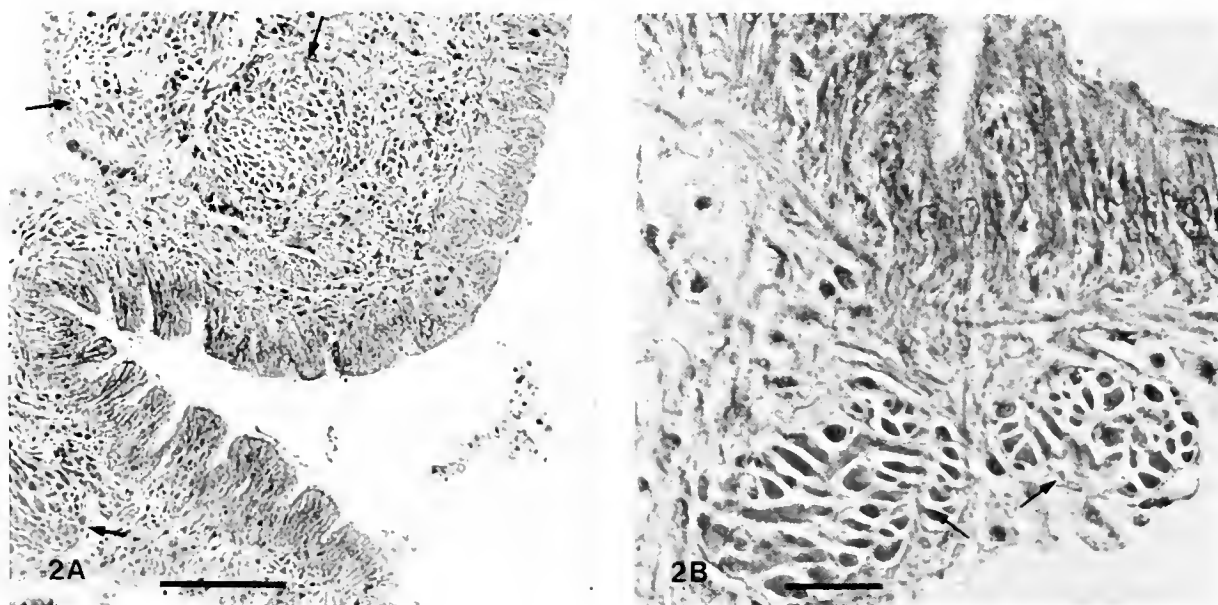
Figure 2. Fibrous tissues of infected oysters: 2A, fibrous tissue development in the gill (←) (bar = 200μm); 2B, fibrous tissue at a higher magnification (←) (bar = 100 μm).
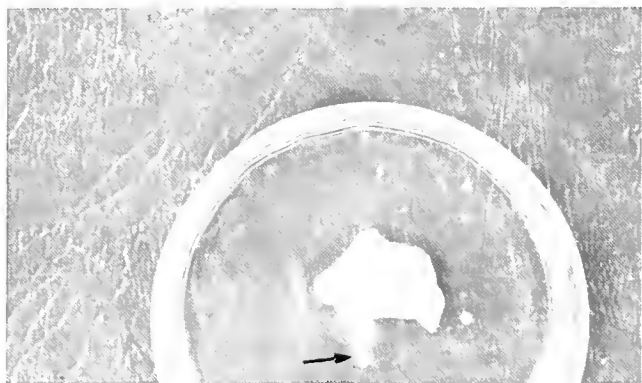
Figure 3. Fungal colony (←) from an infested oyster shell; incubated in seawater for 3 weeks at 15°C.

4A

4B
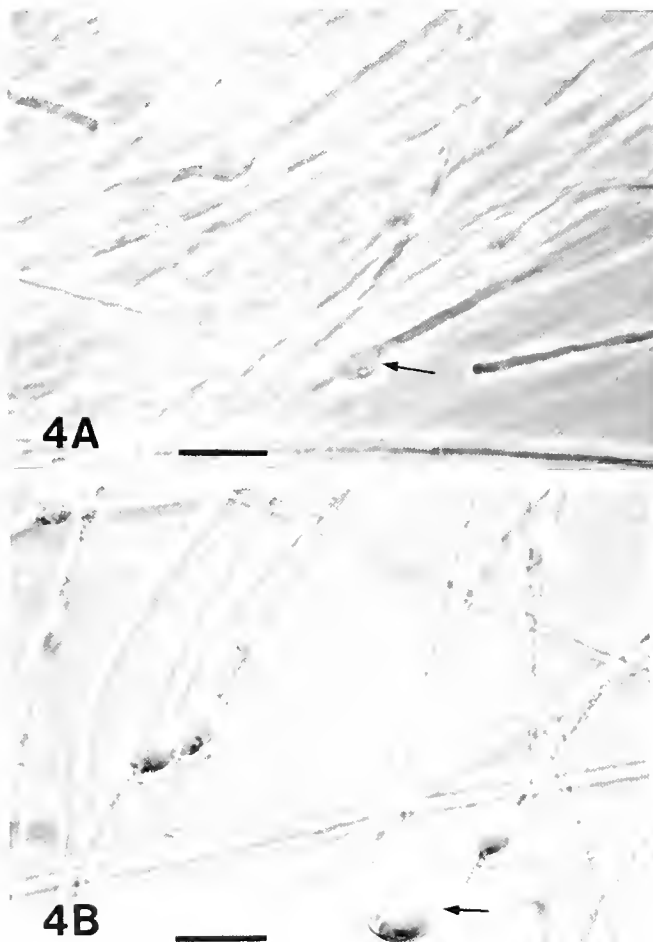
Figure 4. Cultures of the isolated organism in a yeast/peptone medium at 15°C: 4A, 7-day-old culture (note the ovoid swellings at irregular intervals, arrowed); 4B, 4-month-old culture at 5°C (note an increase in number and size of the enlargements of the mycelia; some are developing into spherical chlamydospores[←]). Bar = 20 μm

An outbreak of the foot disease occurred in populations of the Pacific oyster *Crassostrea gigas* (Thurnberg) off the Canadian west coast in the fall of 1956 (Quayle 1969).

The same organism may cause both shell and foot diseases (Sinderman and Rosenfield 1967, Sprague 1971). Unfortunately, the causative agent of foot disease on the west coast was not identified.

Ostracoblabe implexa was described in relation to shell disease of oysters almost a century ago (Bornet and Flahault 1889), but the isolation was not accomplished until 1971 by Alderman and Jones (1971a, b). One of the major characteristics of the organism is the presence of ovoid or spherical swellings in the mycelium (Alderman and Jones 1971b; Alderman 1976, 1980). Our isolate showed similar ovoid enlargements and fine structure of the prochlamydospore as described in the literature. Our results further demonstrated the morphogenesis of the chlamydospore during incubation at low temperature. No sexual reproductive phase was observed. *Ostracoblabe implexa* has been placed in the phycomycetes but its exact taxonomic position remains to be determined.

SH
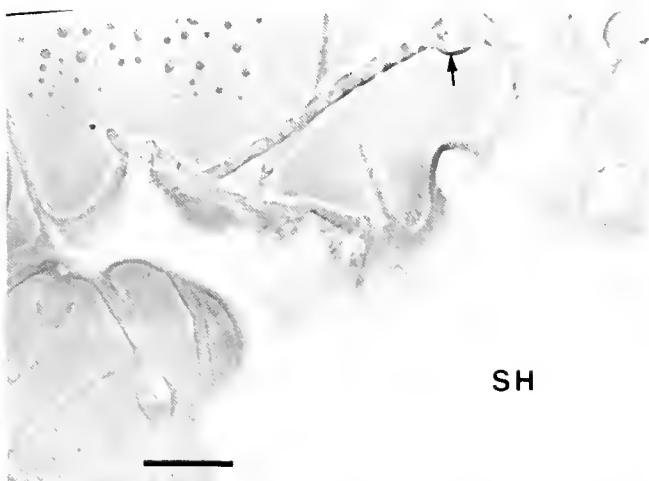
Figure 5. An experimentally infested oyster shell (SH) incubated in seawater for 3 weeks at 15°C. Phase contrast of specimen decalcified by Cat-Ex®. Note the typical ovoid swellings (←). Bar = 20 μm

Figure 6. Electron micrographs of mycelium and prochlamydospores from an isolate grown in a yeast/peptone medium for 7 days at 15°C: 6A, mycelium containing vacuoles and electron-dense bodies; 6B and 6C, ultrathin sections of prochlamydospores; 6D, cross section of prochlamydospores. Note the spores containing inner and outer walls, nucleus, vacuoles, mitochondria, and numerous electron-dense bodies. (N, nucleus; OW, outer wall; IW, inner wall; V, vacuole; ED, electron-dense bodies; M, mitochondria; ER, endoplasmic reticulum) Bar = 1μm
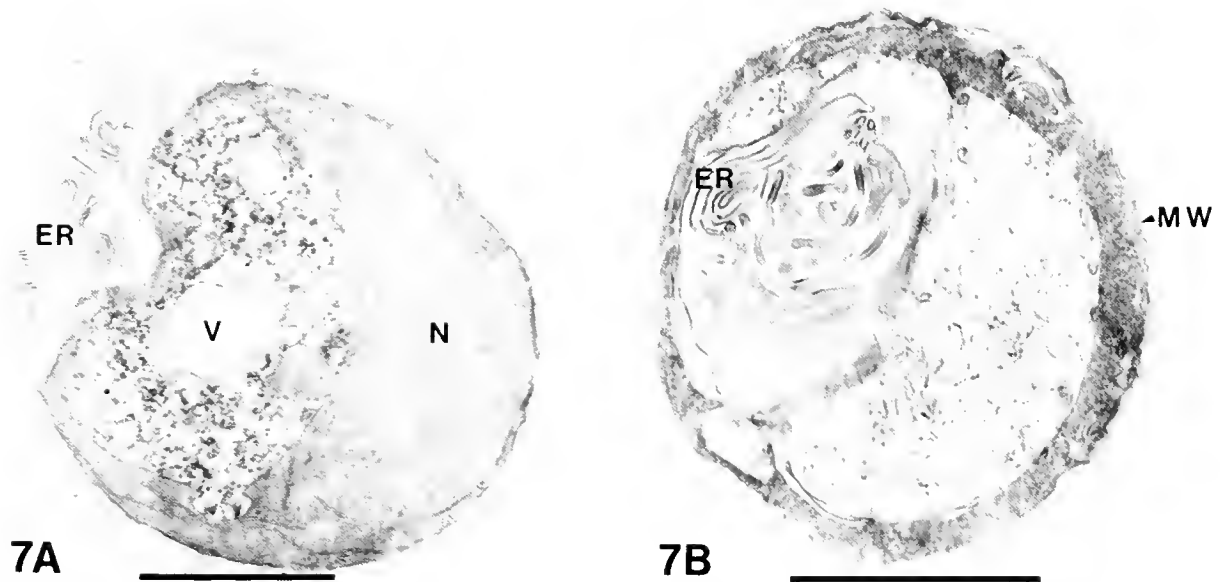
Figure 7A and 7B. Chlamydospores from a culture which had been incubated at 5°C for 4 weeks. Note the curling arrangements of micro-tubules and development of a thick, multilayered wall. (N, nucleus; V, vacuole; MW, multilayered wall; ER, endoplasmic reticulum) Bar = 1 μm

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THE ORIGIN AND EXTENT OF OYSTER REEFS IN
THE JAMES RIVER, VIRGINIA[1]

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ABSTRACT The public oyster grounds (Baylor Survey Grounds) in the James River, VA, were studied with respect to bottom type and oyster density from 1978 to 1981. Approximately 10,118 ha (25,000 acres) were investigated using an electronic positioning system to establish station locations. Bottom types were determined using probing pipes, patent tongs, and an acoustical device. About 17.1% of the bottom was classified as consolidated oyster reef, and 47.5% was moderately productive mud-shell or sand-shell bottoms. The remaining 35.4% was rated as unsuitable for oyster culture. The surface configuration of oyster reef areas in the James River is similar to those in coastal lagoons along the Gulf of Mexico. They are thought to have developed in the James River as they did in the Gulf of Mexico area as sea level rose during the Holocene Period.

KEY WORDS

INTRODUCTION

The naturally productive oyster-growing areas in Virginia were surveyed and set aside for public use in 1894 by Lt. J. B. Baylor (Baylor 1894) and since then have been designated as Baylor Grounds. Statewide, they comprise about 98,324 ha (243,000 acres) with 10,118 ha (25,000 acres) located in the James River, VA (Haven et al. 1981a). The Baylor Survey outlined only broad areas of naturally productive bottoms and did not delineate nor quantify the size or shape of individual oyster reefs. Consequently, many unproductive areas (mud and sand bottoms) were included within the bounds of the survey (Moore 1911, Loosanoff 1931, Haven et al. 1981a).

This paper describes and quantifies the seed-oyster producing regions in James River, VA, within the bounds of the public (Baylor Survey) oyster grounds. It is a portion of a much larger investigation which evaluated the suitability for oyster culture of nearly all public oyster grounds in Virginia (Haven et al. 1981b). The area studied, divided into five zones, is shown in Figures 1 and 2.

Prior to this study there were only two attempts to quantify productive and nonproductive areas within the Baylor Grounds. The first was conducted in 1910 using a chain drag, hand tongs, and a lead line to outline bottom types and quantify oyster density (Moore 1911). Positions were established by sextant bearings and about 10,440 soundings were taken. A second study was conducted between 1973 and 1976 which demonstrated significant changes in oyster density along seven corridors in the James River, but the area of the various bottom types were not determined (Loesch et al. 1975).

The James River has been and continues to be of major importance to the oyster industry in Virginia. Oysters set and survive well there but growth is slow and meat quality is typically poor (Loosanoff 1931, Haven et al. 1981b). Since the mid-1800's, small oysters of less than 7.6 cm (3 in.) in length (termed seed oysters) have been harvested from the river and transplanted to other areas where growth and meat quality improved. In the past 50 years, an estimated 75% or more of the seed oysters planted in Virginia by private interests on leased bottoms came from the James River (Haven et al. 1981b).

From about 1920 to 1945 annual seed-oyster production in the James River averaged about 1,675,000 Virginia bushels (82,346 m^3) (Marshall 1954), and from 1946 to 1961 it averaged between 1.5 to 2.5 million (73,800 to 123,000 m^3). Between 1961 and 1981, however, yearly production fell drastically and in that period it fluctuated between 250,000 and 550,000 bushels (12,300 and 27,075 m^3) (Haven et al. 1981b).

The decline in landings has been associated in part with a decline in demand for seed oysters because of the impact of the oyster pathogen *Haplosporidium nelsoni* (Haskin, Stauber and Makin), commonly called MSX, on adult populations growing in high salinity waters (Haskin et al. 1966, Andrews 1968). An additional cause of the decline in seed production was the low demand for seed resulting from unfavorable economic conditions such as high growing costs and an unstable market for the final product (Haven et al. 1981b). Accompanying the decline in landings was a decline in spatfall intensity which was most severe in the lower half of the seed area (Haven et al. 1981b, Andrews 1982) (Table 1). The cause of this latter decline has not yet been adequately explained. The James River, like most of Chesapeake Bay, has in the past three decades experienced
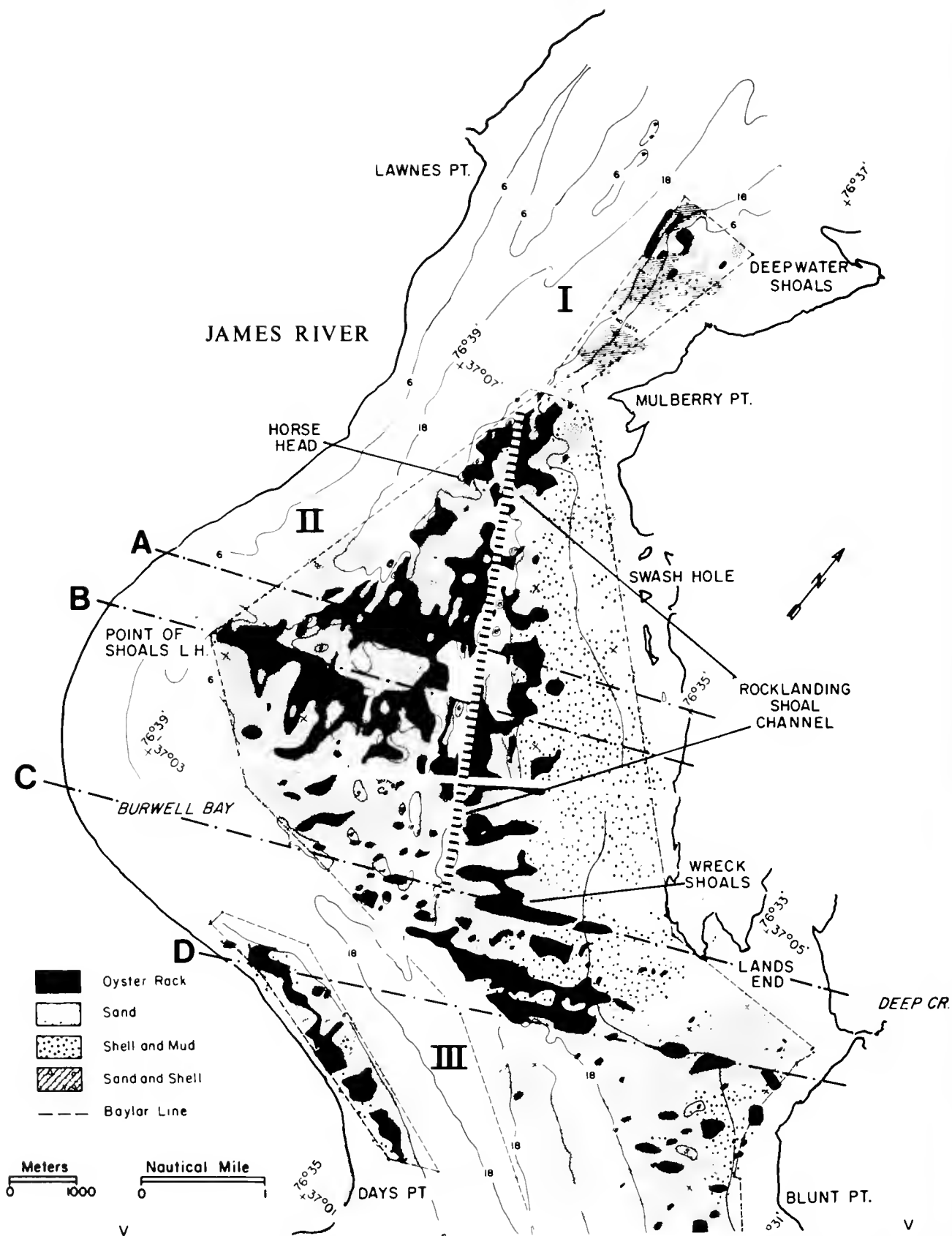
Figure 1. Oyster reefs and other bottom types in the James River, VA. Shown are areas I, II, and III separated by the clear lines and transects A, B, C, and D. Mud bottoms within the bounds of the Baylor areas are unstippled.
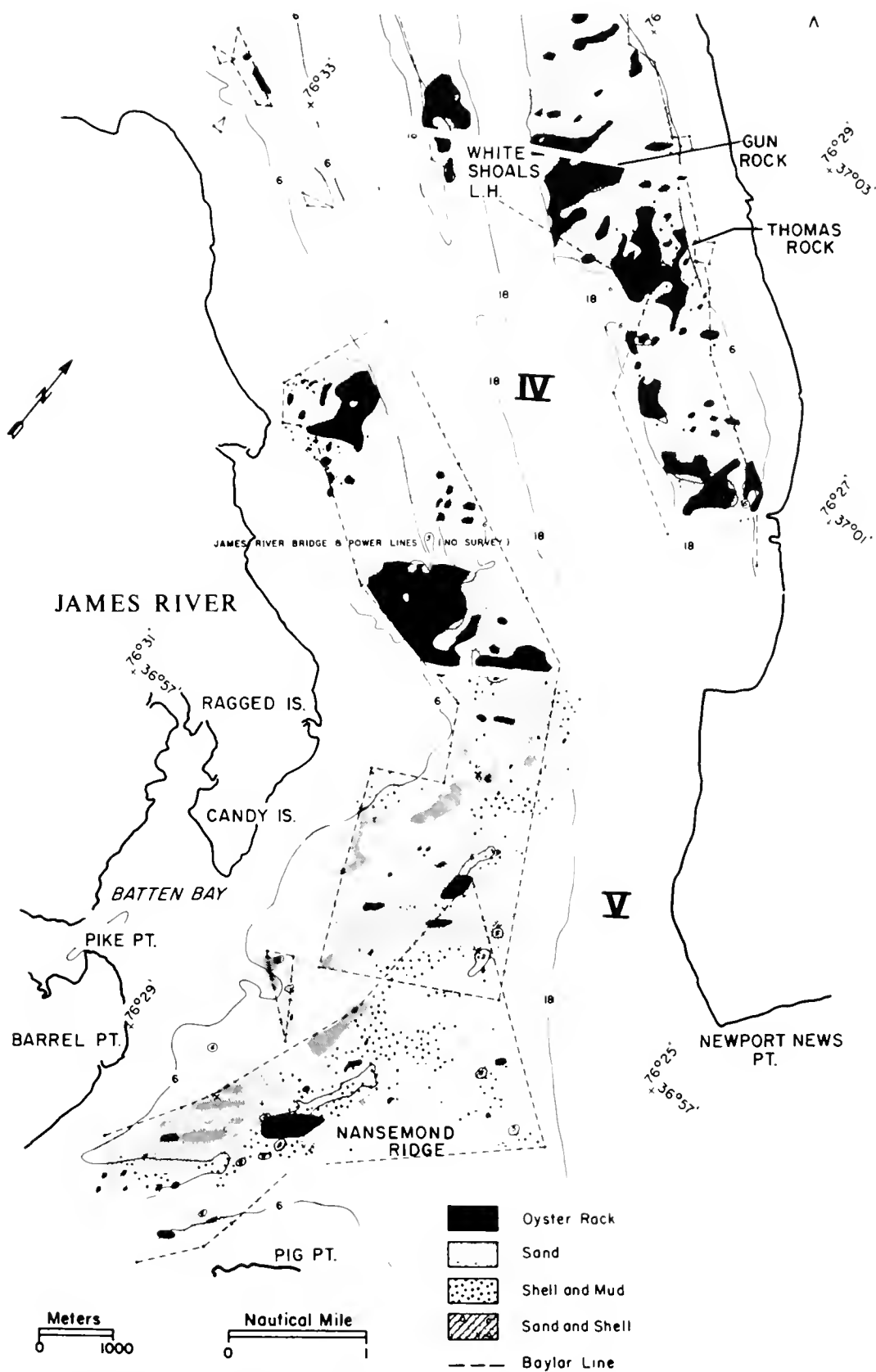
Figure 2. Oyster reefs and other bottom types in the James River, VA. Shown are areas IV and V separated by the clear lines. Mud bottoms within the bounds of the Baylor areas are unstippled.

increased levels of nutrient enrichment, toxic chemicals, sedimentation, and other human alterations (Haven et al. 1981b), all of which may have affected setting of spat.

TABLE 1.

Mean spatfall per Virginia bushel of bottom substrate at representative locations from 1947 to 1980.*

Period	Brown Shoals	Wreck Shoals	Point of Shoals	Deep Water Shoals
1947–1950	718	1901	385	1744
1951–1955	1030	1945	336	872
1956–1960	412	995	––	468
1961–1965	94	298	135	113
1966–1970	27	88	249	334
1971–1975	46	167	82	49
1976–1980	43	199	169	534

*1947–1965 data from Andrews (1982).

Hydrography of the James River

The hydrography of the James River has been the subject of several major studies but many details are still poorly understood. Basically, it is a partially mixed tidal estuary (Pritchard 1953, Nichols 1972b); recent studies suggest it may undergo a cyclic stratification-destratification process related to the neap and spring tidal cycles (Haas 1977).

Published information on salinity from 1949 to 1961 at Deep Water Shoals showed a range from about 2 to 10 ppt, at Wreck Shoals from 7 to 14.5 ppt, at Newport News Point from 12.5 to 18.5 ppt, and at Nansemond Ridge from 13.5 to 19.5 ppt (Table 2). Additional data for all stations from 1963 to 1981 showed a similar range (VIMS unpublished). Freshets occur at irregular intervals in this estuary and 0.0 ppt has been recorded as far downriver as Wreck Shoals (Andrews et al. 1959, Haven et al. 1976). Salinities of 0.0 ppt commonly occur at Deep Water Shoals where oysters are frequently killed by fresh water in the spring of the year (Andrews et al. 1959).

TABLE 2.

Mean salinities (in ppt) in the James River, VA, from 1949 to 1961.*

Season	Stations			
	Deep Water Shoals	Wreck Shoals	Newport News Point	Nansemond Ridge
Spring	2.0	7.0	12.5	13.5
Summer	10.0	14.0	17.5	18.5
Fall	5.0	14.5	18.5	19.5
Winter	––	13.0	16.0	16.5

*Adapted from Stroup and Lynn (1963).

The natural channel in the lower James River lies close to the north shore, near Newport News Point, and toward the south shore in the Burwell Bay area. In the upper estuary near Deep Water Shoals, it is near the center of the river. Rocklanding Shoals Channel was cut through the northern edge of the seed areas and its depth in 1976 was 7.6 m (25 ft) (Figure 1).

The names of individual seed areas in the James River have remained virtually unchanged for over 100 years. For example, the oyster reef known as Deep Water Shoal, marks the upriver limit of commercial production and Nansemond Ridge is the lower limit (Figures 1 and 2). These names can only be used to designate the general location of a seed-producing area because one area grades imperceptibly into another.

MATERIALS AND METHODS

The criterion for defining the naturally productive areas is based on one aspect that is considered of major importance. The naturally productive areas in the James River (those having oysters or shells) have existed in nearly the same location since 1854 (Moore 1911, Marshall 1954). Moreover, as will be discussed later, many probably existed in the same approximate location for much longer periods as was determined for Gulf of Mexico oyster beds (Bouma 1976). This study was designed to detect shells or living oysters in or on the bottom. Their presence was indicative of productive or previously productive bottoms.

The survey vessel was navigated at a speed of about 5.5 km·h^{-1} (3 knots) within the bounds of Baylor Grounds along a series of transects which were delineated using the Raydist® (manufactured by Teledyne Hastings Corp., Hampton, VA) electronic positioning grid system with a precision of ± 2 m. While traversing these transects, the bottom was probed with a 2.5-cm diameter copper pipe every 60 to 90 m to determine bottom type. The probing interval was decreased when the bottom type changed rapidly. Transects were usually about 183 m apart. Studies on bottom types were completed during 1979; sampling for oyster density was carried out in 1981.

The presence or absence of shells and/or oysters between probe stations was monitored continuously with an underwater microphone mounted in a steel frame and dragged on a cable about 37 m behind the vessel. The sounds made by the microphone bouncing over shells or oysters or sliding over sand or mud were amplified and broadcasted. The intensity and frequency of the sounds and the percentage of time the microphone was impacting on shells or oysters or other bottom types between stations were recorded by the operator (Haven et al. 1979). Depths were monitored continuously with a recording fathometer. These latter readings were used to reconstruct four longitudinal profiles across various bottom types.

For each station, Raydist® coordinates, coded information on bottom types obtained with the probe, acoustic information, and depths were recorded on tape using a Teledyne/Hastings printer. Later, the data on the printed tape were plotted on a series of 1:10,000 charts The

charts showed latitude and longitude, 1.8- and 5.5-m (6- and 18-ft) depth contours, outlines of the shorelines, outlines of the Baylor Grounds, and information on bottom types. Subsequently, the boundaries of the various bottom types were outlined on the charts. Areas of various bottom types were determined with a digitizing planimeter.

The following bottom types were described:

Oyster reef: firm bottom, probe penetrated 0 to 5 cm. Shells and oysters were typically abundant. Shells or oysters were detected using the microphone from 75 to 100% of the time between the probe stations.

Sand-shell: The firm bottom consisted largely of unconsolidated shell; probe operator detected the gritty texture of sand. Shells or oysters were detected using the microphone from 25 to 75% of the time.

Mud-shell: The probe operator detected a moderately firm crust over a soft bottom. The probe, after penetrating the crust, could be thrust at least 0.2 to 0.6 m further into the bottom. Unconsolidated shells or live oysters were usually detected using the microphone from 25 to 75% of the time between stations.

Mud: On these soft bottoms the probe could often be pushed almost 1 m into the bottom with little effort. They consisted largely of mixtures of silts and clays with some sand (Nichols 1972a). Shells and oysters were usually absent, or very few as determined using the microphone.

Sand: These were firm bottoms, and the probe typically did not penetrate more than 2 cm. Few shells or oysters were detected using the probe or underwater microphone. Probe operator detected gritty texture of sand.

After the bottom types were outlined on charts, the bottoms in Areas II and III (Figure 1) were sampled with hydraulically operated patent tongs. Each tong grab sampled an area of 0.68 m^2 (7.29 ft^2) and penetrated the bottom about 10 cm on oyster reef and 30.5 cm on mud bottoms; each sample consisted of at least one-half of a Virginia bushel (one Virginia bushel = 0.05 m^3). A total of 476 sampling stations were randomly chosen along transects defined using the Raydist® system. Data from each grab were recorded as follows: numbers and volumes (in U.S. quarts where 1 quart = 0.91 liter) of oysters exclusive the current year's spat, volume in quarts of shells and fragments, and estimates of the percentage of unburied shell as identified by the presence of fouling organisms. These data were used to calculate oyster density (number · m^{-2}) and the percentage of each grab that was composed of shells and shell fragments.

A preliminary analysis of data on oyster density indicated a skewed distribution with a high percentage of zero values; therefore, densities were analyzed for possible significant differences in modal values using the Mann-Whitney test for nonparametric data (Sokal and Rohlf 1981). Oyster distribution obtained in this study was compared to distribution found in 1910 by Moore (1911).

National Oceanic and Atmospheric Administration (NOAA) charts 12248 and 12222 (1:40,000) were used in this study to outline depth contours and shorelines. Because these charts show depths in feet and distances in nautical miles, these same units are used to delineate depth contours and distances shown in the illustrations and in some of the tabular material. In the text the following conversions are used: the standard 6- and 18-ft contour depths are 1.8 and 5.5 m, respectively. One nautical mile (6,000 ft) is equal to 1.83 km.

RESULTS

Reef Areas

Areas classified as *oyster reef* show distinctive outlines in different parts of the estuary. In Area I six small reefs existing near the channel are generally elongate and parallel to the axis of the estuary and to the currents. They occur at depths ranging from 1.8 m to more than 5.5 m (Figure 1).

Area II is characterized by larger oyster reefs, most of which differ in shape from those in Area I (Figure 1). On the northeastern side of Rocklanding Channel, they begin about 1.4 km offshore (beyond the 1.8-m contour) and extend to Rocklanding Channel. Many are extensive and appear to be oriented parallel to the current and the axis of the river. Usually, however, there is an almost equal component oriented at right angles to the shore and the current. A similar type of orientation exists on the extensive reef area along the southwestern side of Rocklanding Channel. There the reefs extend to the south for a maximum distance of about 3.7 km, at depths ranging from 1.8 to 5.5 m (Figure 1).

The oyster reefs in Area III are among the most productive in James River, and Rocklanding Shoal Channel passes through the center of this area. On the northeastern side of the natural channel (off Lands End) between the 1.8- and 5.5-m contour intervals, the oyster reef areas form well defined and approximately parallel rows which are approximately at right angles to the axis of the river (and current). Frequently, a reef ends as an isolated series of small reefs still in line with the larger one. On the southwestern side of the estuary in Area III, the oyster reefs are irregular in outline but the trend appears to be parallel to the channel as in Area I. Many are located at depths of less than 1.8 m. This is in contrast to the distribution noted on the northeastern side where most occur between the 1.8- to 5.5-m contour lines (Figure 1).

In Area IV on the northeastern side of the natural channel, which varies in depth from about 7.3 to 15.8 m, irregularly shaped reefs occur between the 1.8- and 5.5-m contours (Figure 2). Here, in contrast to the upriver areas, there is no apparent orientation with respect to the axis of the river (Figure 2). On the southwestern side, the depths of the reef areas differ from those on the opposite side because they exist primarily in less than 1.8 m of water.

They are, however, similar in that they have no apparent orientation.

Oyster reefs in Area V (Figure 2) are usually small and scattered and are oriented at right angles to the axis of the river and are, therefore, similar in this respect to those in Areas I and II. Moreover, they are usually at depths less than 1.8 m as are most reefs on the southwestern side of this estuary.

Other Bottom Types

In Areas I through IV, *sand-shell* bottoms generally occur inshore of oyster reef areas and often extend into the inshore margin of Baylor Grounds; in Area V, where sand-shell bottoms are scarce, they occur largely between the reefs. Areas of *mud-shell* are the most extensive bottom type in Areas II, III and IV and they occur offshore of sand-shell bottoms. Oyster reefs in all zones are usually surrounded by this type of bottom.

Sand bottoms are not common in the James River Baylor Grounds; when they do occur, they are generally located inshore of sand-shell areas. *Mud* bottoms are extensive and occur in all five segments as large irregular zones between shelled areas and in the deeper channels (Figures 1 and 2).

Acreage of Subaqueous Bottom Types

Mud-shell bottoms were the most extensive and totaled 29.8% (3,030 ha) of the Baylor Grounds surveyed (10,178 ha). *Oyster reefs* and *sand-shell* are about equally abundant and comprise 17.1% and 17.7% (1, 744 and 1,800 ha), respectively, of the total area. Therefore, about 64.6% (or 6,574 ha) of the Baylor Grounds in the James River can be classified as productive or potentially productive (Table 3).

The nonproductive *mud, sand,* and *buried-shell* bottoms make up 35.4% (3,604 ha) of the total 10,178-ha area. These latter types have little, if any, potential for oyster culture.

Oyster and Shell Densities

Patent-tong sampling showed a wide variation in oyster density on the various types of bottom. This was expected because a previous study during 1973 and 1974 showed that oyster distribution in the James River was typically noncontiguous (Loesch et al. 1975). The present study showed that oyster densities on all bottom types ranged from 0 to 274 oysters·m^{-2} (Table 4). Oyster-reef bottoms had the highest mean density and ranged from a mean of 34.8·m^{-2} in Area II to 28.0·m^{-2} in Area III. Sand-shell and mud-shell bottoms supported about 50 to 75% fewer oysters. No oysters were recovered in eight samples taken in Area II on mud and sand bottoms. On similar substrates in Area III, oyster densities ranged from 2.2 to 10.7·m^{-2}. This latter value, discussed later, seems atypical.

A statistical analysis using the Mann-Whitney test for nonparametric data (Sokal and Rohlf 1981) showed that the modal grouping for oyster density (Table 4) on oyster-reef areas was significantly higher than for mud-shell and sand-shell bottoms in Area II (Table 5). Mud-shell bottoms have a significantly higher modal grouping than sand-shell. No oysters were found on sand or mud bottoms (Table 4).

In Area III, oyster-reef bottoms have a modal grouping of oyster densities higher than all bottom types tested (Table 5). Sand-shell bottoms were significantly higher than mud-shell, and both have a modal grouping higher than sand. Mud bottoms seemed to show anomalous situations because oyster densities were higher than those found for sand-shell bottoms. A possible reason for this will be covered in the Discussion section.

Analysis of the patent-tong data showed that bottoms classified as oyster reef (on the basis of data obtained using a probe and sonic gear) also contained the highest content of shell material. In Areas II and III, shells and fragments averaged from 42.8 to 33.9%, by volume, respectively, of the grab's content. The high shell content and high values for oyster density are responsible for the firmness of bottoms classified as oyster reef. In addition, almost half of the shell material on oyster reef bottoms was surface shell which was exposed to the flow of the current (Table 6).

Bottoms that were classified as *mud-shell* or *sand-shell* in Areas II and III differed from *oyster reef* bottoms

TABLE 3.

Areas of various types of bottom in the James River, VA, expressed as hectares and as percent of total in each of the subareas (I–V).

Bottom Type	Total Area (ha) I to V	Size of Each Bottom Type (% Total) in Each Subarea					Percent Total All Areas	
		I	II	III	IV	V		
Oyster Reef	1,744	5.1	28.0	14.1	28.5	2.8	17.1	⎫
Sand-Shell	1,800	35.8	22.6	16.5	5.5	19.9	17.7	⎬ 64.6
Mud-Shell	3,030	14.5	29.7	33.5	31.3	23.7	29.8	⎭
Sand	623	11.6	4.6	6.2	1.5	10.5	6.1	⎫
Soft Mud	2,811	33.0	15.1	29.7	32.8	34.8	27.6	⎬ 35.4
Buried Shell	170	0	0	< 0.1	0.4	8.3	1.7	⎭
Total hectares	10,178	298	2533	3903	1466	1978		

because they had smaller volumes of shell material and lower percentages of surface shell; they were less consolidated and more scattered.

TABLE 4.

Density of oysters collected with patent tongs in the James River seed area.*

Bottom Types	Area II			Area III		
	N	Mean	Range	N	Mean	Range
Oyster Reef	19	34.82	0 to 165.76	66	27.98	0 to 273.81
Sand-Shell	27	9.0	0 to 109.52	63	6.48	0 to 35.52
Mud-Shell	19	13.40	0 to 118.90	188	5.75	0 to 59.20
Sand	4	0		21	2.18	0 to 41.44
Mud	4	0		73	10.72	0 to 112.48

*From Statistical Summary of Means and Range (1981).

TABLE 5.

A statistical comparison using the Mann-Whitney test of modal grouping of oyster density (m^2) in Areas II and III in the James River, VA. (Mean values for numbers of oysters per m^2 are shown in Table 3.)

Bottom Type	Levels of Significance
	Area II
Oyster reef versus mud-shell	Difference significant at $0.25 > P > 0.01$
Oyster reef versus sand-shell	Difference significant at $0.01 > P > 0.001$
Mud-shell versus sand-shell	Difference significant at $P = 0.01$
	Area III
Oyster reef versus mud-shell	Difference significant at $P < 0.001$
Oyster reef versus sand-shell	Difference signfiicant at $P < 0.001$
Oyster reef versus sand	Difference significant at $P < 0.001$
Mud-shell versus sand-shell	Difference significant at $0.01 > P > 0.001$
Mud-shell versus sand	Difference significant at $0.05 > P > 0.02$
Sand-shell versus mud	Difference significant at $0.01 > P > 0.001$
Mud versus sand	Not significant at $P = 0.10$
Mud-shell versus mud	Not significant at $P = 0.10$

Transects

Elevations and slopes were studied across the oyster reefs, or shoals, on four transects in the area near Point of Shoals Light (Figures 1 and 3). Those transects crossed productive oyster reefs such as Wreck Shoal and Point of Shoals. The overall slope from the channel to the sandy margins along the shore ranges from about 0.04 to 0.11 m (0.13 to 0.35 ft) vertically for each 30.5 m (100 ft)

horizontal distance (slopes: 1:769 to 1:286, respectively). Frequently, the elevation of the bottom from a nonproductive slough to a productive shelled area was less than 0.30 m (1 ft) vertically for every 30.5 m (100 ft) horizontally. Very steep slopes occur adjacent to the channel or mud sloughs where they join productive oyster-reef or mud-shell substrates. These sharp slopes may be as large as 4.6 m (15 ft) vertically in 30.5 m (100 ft) horizontally (a slope of 1:6.7). *Sand-shell* bottoms occur as flat areas and are usually near the shore.

DISCUSSION

Samples obtained with patent tongs in Areas II and III confirmed observations made using a bottom probe, acoustic gear, and fathometer. *Oyster reef* bottoms had higher densities of oysters and shell material. *Sand-shell* and *mud-shell* bottoms had lower densities of oysters and shells. *Sand* bottoms seldom contained shells or oysters. *Mud* bottoms, while definitely soft, sometimes contained significant numbers of oysters.

The surface outlines of oyster reefs in the James River may be separated into four types which closely resemble those that occur in lagoonal systems of the Gulf of Mexico (Graves 1905, Hedgpeth 1953, Price 1954, Scott 1968, Bouma 1976). The **longitudinal** type, for example, is represented in the James River by those shown on Area 1 where tidal currents are rapid over shoal bottoms. The **large irregular** type is common throughout the estuary and has two components; one is at a right angle to the axis of the river and a second is parallel to the axis (Area II). A third type, termed a **transverse** reef, is long and lies at right angles to the current as seen in Area II off Lands End (Figure 1). The last type, without any obvious shape, is termed a **pancake** reef (Scott 1968); these are common in Area V (Figure 2).

While those bottoms that were classified as *sand-shell* and *mud-shell* in the James River support live oysters and are moderately productive, we do not believe them to be long-term features of the estuary at specific locations as are oyster reef areas. This concept was originally discussed by Moore (1911) who stated that the boundaries of the highly productive areas in the James River seed area, which approximate our oyster reef classification, were originally sharply marked and separated from the barren (*mud* or *sand*) bottoms. Moore (1911) speculated that operations by man (harvesting activities and culling of the catch) over the years were responsible for scattering shells and oysters between the reefs and onto otherwise barren bottoms. The atypical value of 10.7 oysters·m^{-2} on *mud* bottoms shown for Area III (Table 4) probably resulted from this activity.

Oysters do not grow or survive well on *sand* and *mud* bottoms because of several physical factors. *Mud* bottoms in the James River are areas of active sedimentation (Nichols 1972a); in that environment, oysters may be covered with sediment faster than they can grow (MacKenzie 1983).

TABLE 6.

Number of oysters per m^2, exclusive of 1979 spat set, and amounts of surface and buried shells on
five bottom types in the James River, VA (August 1979).

Bottom Type	Number Sampled	Mean Number $\cdot m^{-2}$	Percent Shell	Percent Surface Shell	Percent of Sample with Surface Shell
		Area II			
Oyster reef	19	34.8	42.8	47.7	94.7
Sand-shell	27	9.0	23.1	16.1	48.1
Mud-shell	19	13.4	16.0	17.9	36.8
Sand	4	0.0	12.0	0.0	0.0
Mud	4	0.0	5.1	0.0	0.0
		Area III			
Oyster reef	66	27.98	33.9	41.8	90.1
Sand-shell	63	6.48	23.1	25.0	81.0
Mud-shell	188	5.75	11.8	13.2	41.0
Sand	21	2.18	9.9	8.1	9.0
Mud	73	10.72	6.8	8.5	8.0
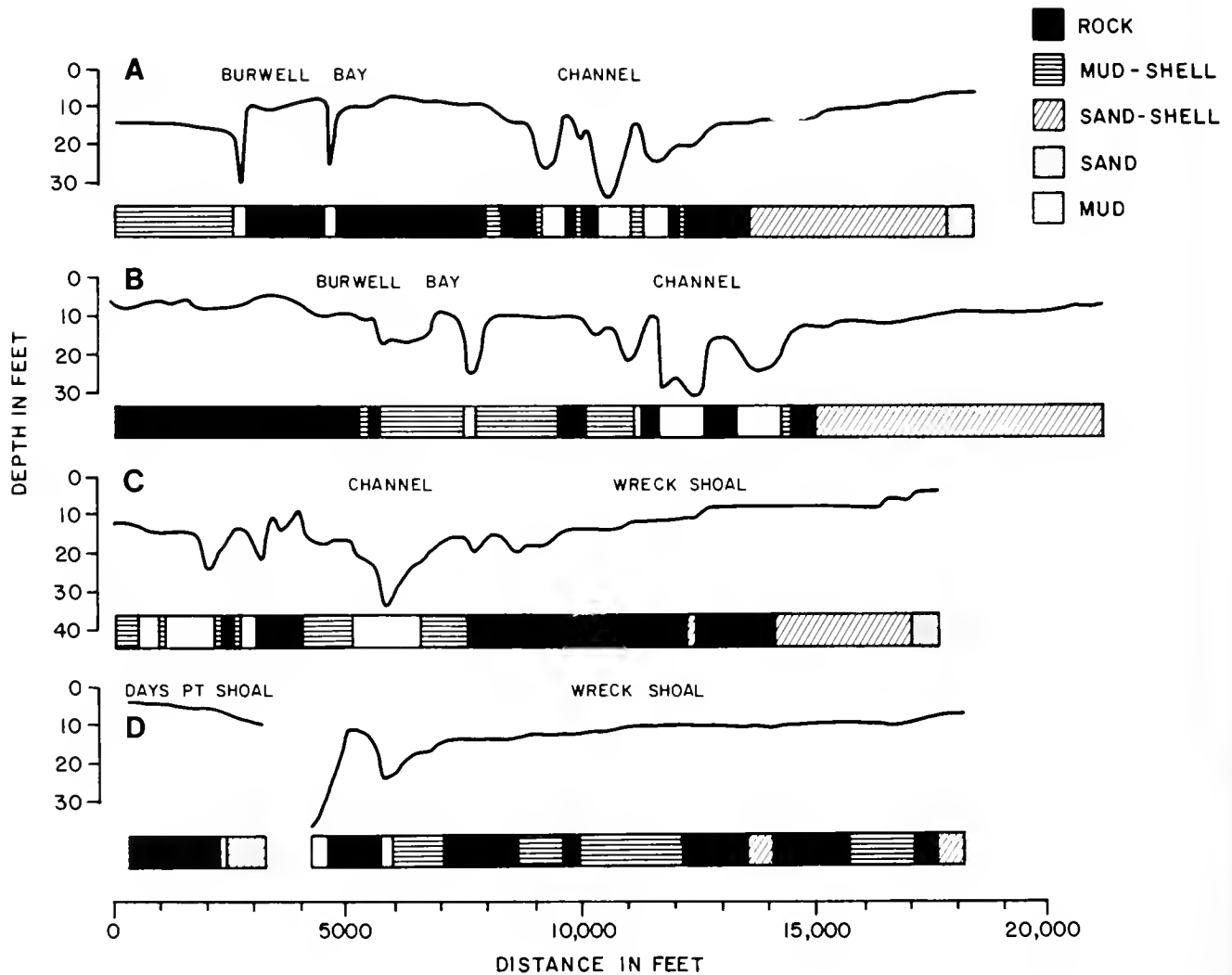
Figure 3. Longitudinal profile of various oyster bottom types along transects A, B, C and D (see Figures 1 and 2).

Sand bottoms, while firm, offer an unstable, shifting substrate and sand grains are abrasive and difficult to void from the mantle cavity when washed in by wave or current forces. We speculate that conditions for recruitment and growth on *mud-shell* or *sand-shell* areas may often be marginal or they may fluctuate to a greater degree than *oyster reef* areas.

The extent and depth of buried oyster shell deposits below the reefs in the James River are not known; however, about 2.0×10^6 m³ of buried oyster shells were dredged commercially between 1963 and 1969 from the southern side of this estuary approximately 6 km southwest of Newport News Point (Figure 2) (Va. Comm. Fish. Rept. 1969, Haven et al. 1981b). An early study of lagoonal systems in the Gulf of Mexico showed that exposed oyster reefs often extended down into the sediments for at least 2.7 m (Norris 1953). Later Bouma (1976), working in the same area, related reef oyster formation to the world-wide rise in sea level during the Holocene Period (Emery and Uchupi 1972). He concluded that most of the present-day oyster reefs in San Antonio Bay exist on top of old reefs that started to grow about 9,000 years ago in the former river cuts incised in late Pleistocene deposits as the sea level began to rise. He demonstrated that shell deposits extended as deep as 21 m (69 ft) below the sediment surface and his 14_C data showed ages of buried shell from 1,500 to 9,000 years. Bouma (1976) also stated that many surface reefs were probably connected or adjacent to buried shell deposits.

The James River Basin and Gulf of Mexico areas experienced the same rise in sea level during the Holocene Period. In relation to this event, the James River Basin flooded with seawater between 9,000 and 6,500 years ago. The original flooding occurred along the axis of the river as defined by the deeper channels that today range in depth from 8 to 29 m (Nichols 1972a). The sea level has increased about 0.6 m in the James River between 1854 and 1954.

It has yet to be determined how far oyster reefs extend into bottom sediments in the study area; however, on the basis of similarity in shape of oyster reefs in the James River and Gulf of Mexico areas and the similar geological histories, we speculate that oyster reefs in the river are underlain with shell deposits of varying thickness and that the reefs evolved as they did in the Gulf areas from old shore or bottom features as sea level rose.

There have been slow changes in water depth over oyster reefs in the James River over the last century. Marshall (1954), using depth data from U.S. Hydrographic charts from 1854-55 to 1943-48, stated that considerable variations existed in the physiographic changes in the surfaces of the seed beds (tops of the oyster reefs) during that period. At most points depth comparisons over the 100-year period, after allowing for the increase in sea level, indicated a decline in elevation of about 0.18 m (0.6 ft). He speculated that this decline was the net effect of both natural phenomena and fishery activities.

Our data, when compared with those obtained by Moore in 1910 (Moore 1911), suggest no major differences in oyster density in 1911 and 1981. Moore reported oyster densities for about 590 locations in the seed area and used them to separate bottoms into five classes (Table 7). Those classifications were a combination of numerical data on oyster density coupled with Moore's concept of how many oysters a waterman needed to harvest during a 9-hr day at the former price of $0.20 to $0.30/bu for seed and $0.45/bu for market oysters. Certain of his categories are still valid. Moore's *barren* category is comparable to our mud or sand classifications; both have a very low potential for growing oysters. Moore's *dense growth* is equivalent to our oyster reef classification, and our definition of productive bottoms (oyster reefs and mud-shell or sand-shell bottoms) is comparable to Moore's *dense, scattered, very scattered* and *depleted* categories (Table 7).

TABLE 7.

Classification of oyster bottoms in the James River, VA.*

Oyster Density	Oyster Harvest in Virginia Bushels by a Tonger in a 9-hour Day	
	Seed Oysters	Market Oysters
Barren (no shell or oysters)	9	9
Depleted	4	3
Very scattering (scattered)	4 – 8	3 – 5
Scattering (scattered)	8 – 12	5 – 8
Dense	12	8

*Classification from Moore (1911).

Using the preceding categories, the following comparisons are made (Table 8). In 1910 (Moore 1911), mean oyster densities on *dense* bottoms ranged from 26.9 to 35.4 oysters·m⁻² in Area II. In contrast, our randomly collected reef samples in 1981 showed a similar density of 34.8·m⁻². Mean oyster densities on *scattered* to *depleted* bottoms in Moore's study (1911) ranged from nearly zero to a maximum of 20.2·m⁻² while mean densities for comparable bottom types in 1981 ranged from 9.0 to 13.4·m⁻². In Area III, three stations in Moore's study ranged in density from 32.9 to 57.0·m⁻²; our mean density for oyster reefs in the same general area was 28.0·m⁻². Mean densities in areas of *scattered* to *depleted* bottoms ranged from zero to 33.1·m⁻² in the early 1900's; our density data showed a mean range of 2.2 to 10.7·m⁻² (Table 7). The overall similarities in density for *dense* and *reef* bottom types were unexpected because of the decline in setting intensity in the James River that began in 1960 (Haven et al. 1981b). We speculate that, in 1910, the intense harvest may have depleted the beds to low levels, even when oysters were setting at a much higher rate.

TABLE 8.

Mean densities of oysters on various bottom types in the James River, VA, 1910–1981. (Locations shown in Figure 1.)

1910 (Moore 1911)			1981 (Present Study)		
Oyster Reefs	Growth Type	Oysters/m^2	Location	Substrate	Oysters/m^2
Area II					
Horse Head	Dense	35.4	Horse Head to	Oyster reef	34.8
	Scattering	15.4	Point of Shoals	Sand-shell	9.0
	Very Scattering	20.2		Mud-shell	13.4
	Depleted	0.1		Sand	0
				Mud	0
Point of Shoals	Dense	26.9			
	Scattering	13.1			
	Very Scattering	5.5			
	Depleted	2.0			
Area III					
Wreck Shoals	Dense	48.6	Wreck Shoals to	Oyster reef	28.0
	Scattering	0	Thomas Rock	Sand-shell	6.5
	Very Scattering	0		Mud-shell	5.8
	Depleted	0		Sand	2.2
				Mud	10.7
White Shoal	Dense	57.0			
	Scattering	0			
	Very Scattering	10.3			
	Depleted	9.1			
Thomas Rock	Dense	32.9			
	Scattering	33.1			
	Very Scattering	22.4			
	Depleted	15.4			

Further inspection of Moore's data reveals that the present productive areas in the James River are in the same approximate area as they were in 1910; however, the areas of productive and potentially productive bottoms may have increased since 1910. To show this, we compared the geometric area of the top four categories shown by Moore (Table 7) with our *mud-shell, sand-shell* and *oyster reef* categories in Areas II and III. These data showed a total area of 2,722 ha (6,727 acres) in 1910 and 4,534 ha (11,204 acres) in 1980, a gain of about 60%. While this cannot be considered conclusive because of the nature of the original data set, the positive direction is suggestive. We attribute the probable increase to the effect of culling unwanted shells and small oysters onto unproductive sand and mud bottoms from 1910 to 1981.

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GENETIC DIFFERENTIATION AND POPULATION STRUCTURE OF THE AMERICAN OYSTER *CRASSOSTREA VIRGINICA* (GMELIN) IN CHESAPEAKE BAY

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ABSTRACT Genetic variation and differentiation were studied among 10 oyster bars of the American oyster *Crassostrea virginica* (Gmelin) in Chesapeake Bay. The observed heterozygosity ranged from 0.195 to 0.230 while the proportion of polymorphic structural loci ranged from 0.483 to 0.552 among demes. The genetic similarities among oyster bars averaged 99% suggesting little genetic differentiation; however, F_{st} statistics revealed that 23 of 41 alleles were significantly different among demes, suggesting spatial heterogeneity among oyster bars within Chesapeake Bay. Principle component and step-wise multivariate discriminant analyses of the 28 most common alleles indicated that the 10 oyster bars could be partitioned into four different latitudinal groups (e.g., subpopulations). The four subpopulations are probably maintained by a balance between the migration of planktonic oyster larvae and the adaptation of genotypes to local environmental conditions.

KEY WORDS: allelic variation, Chesapeake Bay, *Crassostrea virginica*, multivariate analysis, oyster bars, protein electrophoresis, subpopulations

INTRODUCTION

The American oyster *Crassostrea virginica* (Gmelin) is an oviparous, dioecious bivalve. Its planktonic larval stage lasts from two to three weeks and provides ample opportunity for zygotic dispersion (Galtsoff 1964). Large populations of sedentary adults of *C. virginica* are present in Chesapeake Bay. Consequently, the possibility of genetic differentiation between populations by genetic drift can be discounted. In this study, I have attempted to delineate between two theories concerning population structure of *C. virginica* in the bay. The water circulation patterns within the bay and the long planktonic larval stage provide the potential for extensive gene flow among contiguous oyster demes. These factors should contribute to high levels of genetic similarity among oyster bars throughout the latitudinal 240-km range of *C. virginica* in Chesapeake Bay. This would suggest that the bay contains a single panmictic oyster population. Alternatively, if selection pressure was great enough to minimize the effect of gene flow among oyster demes or if larval dispersal was not as wide spread as suggested, then geographic variation in allele frequencies could occur among various regions within Chesapeake Bay. This effect would produce subpopulations (i.e., random mating within groups) of the oyster in the bay instead of a single panmictic population.

Examination of the population structure can be approached through biochemical genetic studies using protein electrophoresis on natural populations which will provide information on gene and genotypic frequencies of structural loci (Powell 1975, Selander 1976). Such information may provide evidence for selection in natural popula-

tions in the form of macrogeographical clines in gene frequency (e.g., spatial changes of allele frequencies with concomitant geographical variation [Koehn 1969, Powell 1971, Schopf and Gooch 1971]); microgeographical clines in gene frequencies (e.g., changes in allele frequencies with concomitant microgeographic gradients or with local environmental heterogeneity [Balegot 1971, Hamrick and Allard 1972, Koehn et al. 1973]); temporal clines in gene frequency (i.e., a progressive change in allele frequencies with year-class or increasing age [Fujino and Kang 1968, Koehn et al. 1971, 1976, 1980, Tinkle and Selander 1973]); and among-locus discordance in patterns of geographical variation (Williams et al. 1973, Christiansen and Frydenberg 1974). In this analysis, 32 structural loci were examined in *C. virginica* with respect to levels of genetic variation and genetic differentiation among oysters bars in Chesapeake Bay. The genic variation was then examined with respect to environmental and geographical variations in the bay, and to among-locus discordance between sampling localities.

Environmental Variation in Chesapeake Bay

Oceanic water moves along the lower water column of Chesapeake Bay in a northerly direction to the head of the bay. Fresh water enters the bay from tributaries and flows in a southerly direction along the upper water column. This opposite flow of fresh- and salt water at different depths in the water column results in macro- and microgeographical salinity gradients. High salinities are found in the deep water layers and lower regions of the bay while lower salinities are found in the surface water layers and upper regions of the bay (Whaley and Hopkins 1952, Stroup and Lynn 1963). This water circulation pattern may be the reason why there are no large spatial gradients in water temperature. Chesapeake Bay does experience seasonal

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climatic variation. Winter surface water often freezes while summer surface water temperatures may reach 30°C simultaneously for all regions of the bay.

MATERIALS AND METHODS

Oyster Bars and Geographical Variation

The oyster samples used in this study were dredged from ten oyster bars from various depths and regions of Chesapeake Bay and its tributaries (Figure 1, Table 1). Only adult oysters of $\geq$ 6 cm length were used. Individuals smaller than 6 cm were not analyzed because of the possibility of genotypic and age (size)-dependent interactions which have been reported between marine bivalves (Koehn et al. 1973, Mitton et al. 1973, Boyer 1974, Tracey et al. 1975, Singh and Zouros 1978, Zouros et al. 1980). All samples were transported to the Marine Products Laboratory, Center for Environmental and Estuarine Studies, University of Maryland, where they were stored at –20°C until analyzed by starch gel electrophoresis. Both recruitment of new individuals and ambient water conditions varied between the collecting localities.

The spatial distribution of natural oyster bars in Chesapeake Bay ranges from the Swan Point site (upper bay) to the James River (lower bay). This constitutes a latitudinal geographic distance of approximately 240 km. The mean water depths at the ten oyster bars sampled in this study ranged from 0.3 to 6.1 m. A salinity gradient also exists among the ten collecting localities, ranging from a mean of 8.5 ppt at the Swan Point site to 17.5 ppt in Pocomoke Sound. A very slight thermal cline in the annual mean water temperature appears among the oyster bars which ranges from 13.0°C at the Swan Point site to 15.5°C in the James River (Table 1).

Sample Preparation, Electrophoresis and Protein Staining Systems

Approximately 0.5 g of either adductor muscle or stomach tissue was extracted from each individual, placed into a test tube containing 1.0 mℓ of distilled water and homogenized with a glass rod. This crude extract was centrifuged at 5,000 rpm for 2 min. The supernatant was then absorbed on cellulose wicks which were set into a starch gel matrix. The methods of horizontal starch gel electrophoresis of oyster samples including buffer solutions and staining solutions are as previously described (Buroker et al. 1975, 1979a, b). the 21 protein-staining systems used in this study were: acid phosphatase (*AcP*), adenine kinase (*Adk*), aldolase (*Ald*), aminopeptidase (*Ap*), aspartate aminotransferase (*Aat*), esterase (*Est*), alphaglycerophosphate dehydrogenase (*aGlypd*), glyceraldehyde 3-phosphate dehydrogenase (*Gly3pd*), hexokinase (*Hk*), isocitrate dehydrogenase (*Idh*), leucine aminopeptidase (*Lap*), malate dehydrogenase (*Mdh*), malic enzyme (*Me*), mannose phosphate isomerase (*Mpi*), muscle protein (*Mp*), 6-phosphogluconate dehydrogenase (*6Pgd*), phosphoglucose isomerase

(*Pgi*), phosphoglucomutase (*Pgm*), sorbitol dehydrogenase (*Sdh*), tetrazolium oxidase (*To*), and xanthine dehydrogenase (*Xdh*). In this study the electrophoretic analyses of soluble proteins reflected 32 structural loci. These loci were selected on the basis of available staining procedures and clarity of protein banding. Two polymorphic loci (*AcP–3* and *Sdh*) could not be resolved for all collecting localities.

Statistical Analyses

The inbreeding coefficient is the correlation between random gametes within subdivisions relative to gametes of the total population and is a measure of the heterogeneity among the subpopulations (Wright 1940, 1969, 1978). The variation in allele frequency between subpopulations can be used to compute the "effective" inbreeding coefficient (F_{st}). The estimate is

$$F_{st} = \sigma^2_{pi}/\overline{p} \ (1 - \overline{p})$$

where $\overline{p}$ represents the weighted mean, and σ^2_{pi} the weighted sum of the squared deviations of the individual subpopulations gene frequencies from the mean gene frequency divided by the number of subpopulations:

$$\sigma^2_{pi} = \Sigma \ [(\overline{p} - pi)^2/n]$$

Because each allele at a locus has its own values of σ^2_{pi} and $\overline{p}$, F_{st} can be used to test for differential selection between the subpopulations. This statistic has also become widely known and is used as the standardized variance of gene frequency between populations (Cavalli-Sforza 1966).

Two other statistical procedures employed were principle component and discriminant analyses. Principle component analysis is a method of reducing the number of correlated measurement variables into a small set of statistically independent linear combinations having certain unique properties with regard to characterizing individual differences (Overal and Klett 1972, Harris 1975). The method (BMDP-4M; Dixon 1977) was used here to describe biological, environmental and genetic differences among oyster bars in Chesapeake Bay. A stepwise multivariate discriminant analysis (BMDP-7M; Dixon 1977) procedure was used to select those characters which best discriminate oyster subpopulations in the bay.

RESULTS

Genetic Variation among Oyster Bars

The 21 protein-staining systems allowed examination of 32 monomorphic and polymorphic structural loci. The 18 loci which displayed genic variation have been tabulated with relation to the collecting localities (Table 2). The 14 loci for which no genic variation was found are: *AcP–1*, *Adk–2*, *Ald*, *Aat–1*, *Est–2*, *Glypd–2*, *Gly3pdh*, *Hk–1*, *Me*, *Mp–1*, *Mp–2*, *To–1*, *To–2*, and *Xdh*. A summary of the
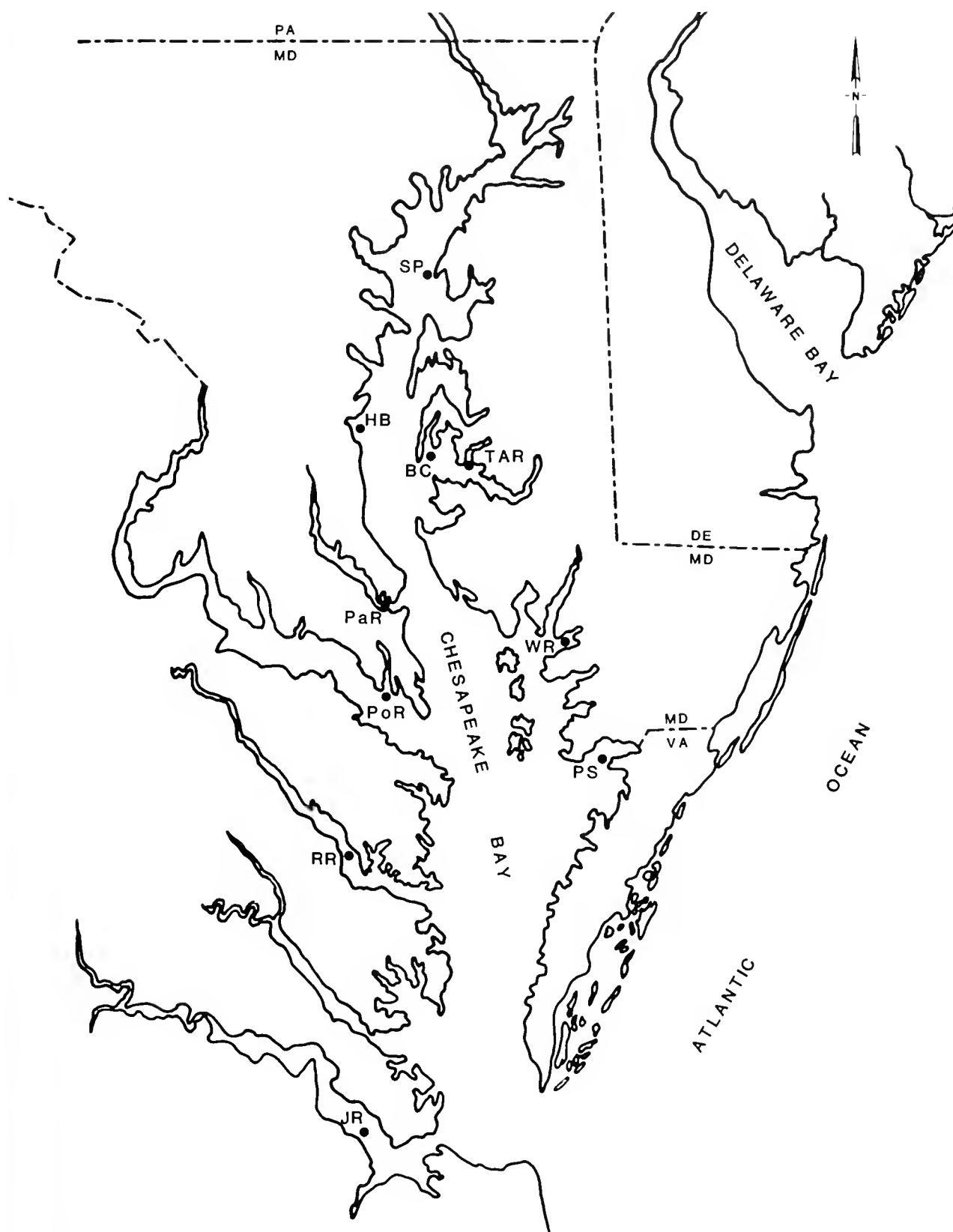
Figure 1. Map of Chesapeake Bay depicting the ten oyster bars sampled in this study. Starting at the head of the bay, the oyster bars are Swan Point (SP), Herring Bay (HB), Broad Creek (BC), Tred Avon River (TAR), Patuxent River (PaR), Wicomico River (WR), Potomac River (PoR), Pocomoke Sound (PS), Rappahanock River (RR), and James River (JR).

TABLE 1.

Biological and ambient environmental parameters from ten oyster bars in various regions of Chesapeake Bay.
The oyster bars range in decreasing latitude from Swan Point, MD, near the head of Chesapeake Bay
to James River, VA, near the mouth of Chesapeake Bay.

	Oyster Bars[1]									
	Maryland								Virginia	
	SP	BC	TAR	HB	PaR	WR	PoR	PS	RR	JR
Mean recruitment (spat/bushel) (1939–1975) Maryland[2] (1961–1975) Virginia[3]	14.6	121.4	32.1	36.4	15.4	63.6	235.5	53.9	73.3	184.3
Mean salinity (ppt)[4] (annual range)	8.5 (3–14)	12.5 (8–18)	12.5 (8–18)	11.0 (4–16)	12.0 (8–18)	14.8 (10–20)	12.8 (8–18)	17.5 (14–23)	13.3 (8–18)	10.1 (7–22)
Water depth (m)[5]	5.2	2.7	4.6	6.1	0.3	4.6	4.6	3.7	3.0	3.7
Mean water temperature (°C)[4] (annual range)	13.0 (1–27)	13.8 (2–28)	13.5 (2–28)	13.6 (2–28)	13.6 (2–28)	13.5 (2–28)	13.9 (2–28)	14.3 (2–29)	15.3 (3–28)	15.5 (2–28)

[1] SP (Swan Point), BC (Broad Creek), TAR (Tred Avon River), HB (Herring Bay), PaR (Patuxent River), WR (Wicomico River), PoR (Potomac River), PS (Pocomoke Sound), RR (Rappahanock River), and JR (James River).
[2] Source: Meritt (1977)
[3] Source: D. Haven, Virginia Inst. Mar. Sci., pers. comm.
[4] Sources: Whaley and Hopkins (1952), Stroup and Lynn (1963).
[5] Source: G. Krantz, Marine Science Laboratory, Crisfield, MD 21817, pers. comm.

TABLE 2.

Genic variation of the American oyster *Crassostrea virginica* among oyster bars from Chesapeake Bay.

Locus	Allele[2] (RM)	Chesapeake Bay Oyster Bars[1]									
		SP	BC	TAR	HB	PaR	WR	PoR	PS	RR	JR
Ap–1	n	180	184	182	182	180	178	182	182	184	182
	103	0.017	0.000	0.000	0.000	0.000	0.006	0.011	0.000	0.000	0.038
	100	0.283	0.397	0.379	0.379	0.428	0.399	0.346	0.341	0.359	0.451
	97	0.228	0.201	0.143	0.143	0.217	0.208	0.148	0.176	0.158	0.198
	94	0.278	0.272	0.247	0.231	0.261	0.197	0.258	0.297	0.212	0.198
	91	0.189	0.130	0.176	0.137	0.094	0.185	0.209	0.148	0.201	0.082
	88	0.006	0.000	0.055	0.110	0.000	0.006	0.027	0.038	0.071	0.033
	H	0.844	0.739	0.758	0.846	0.700	0.753	0.703	0.714	0.891	0.703
	D	0.119	0.040	0.024	0.126	0.010	0.039	−0.059	−0.037	0.178	−0.008
AcP–3	n	— —	148	— —	178	98	72	168	— —	182	184
	120	— —	0.000	— —	0.000	0.000	0.000	0.024	— —	0.000	0.000
	115	— —	0.014	— —	0.035	0.051	0.014	0.065	— —	0.005	0.011
	110	— —	0.507	— —	0.593	0.439	0.444	0.589	— —	0.198	0.446
	108	— —	0.291	— —	0.267	0.398	0.389	0.202	— —	0.357	0.353
	105	— —	0.169	— —	0.105	0.112	0.153	0.119	— —	0.324	0.174
	100	— —	0.020	— —	0.000	0.000	0.000	0.000	— —	0.115	0.016
	H	— —	0.541	— —	0.744	0.857	0.806	0.750	— —	0.593	0.587
	D	— —	−0.142	— —	0.317	0.350	0.576	0.265	— —	−0.171	−0.091
Adk–1	n	180	186	182	184	178	178	182	176	184	184
	104	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.005	0.000
	102	0.078	0.059	0.088	0.103	0.124	0.067	0.088	0.108	0.082	0.082
	100	0.233	0.226	0.198	0.239	0.191	0.315	0.258	0.193	0.196	0.130
	98	0.572	0.597	0.665	0.582	0.640	0.522	0.582	0.625	0.603	0.592
	96	0.117	0.118	0.049	0.076	0.045	0.090	0.071	0.074	0.114	0.185
	94	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
	H	0.600	0.548	0.593	0.674	0.551	0.674	0.637	0.580	0.630	0.652
	D	0.002	−0.047	0.166	0.146	0.027	0.095	0.096	0.045	0.090	0.103

TABLE 2. Genic variation of the American oyster *Crassostrea virginica* among oyster bars from Chesapeake Bay (continued).

Locus	Allele[2] (RM)	Chesapeake Bay Oyster Bars[1]									
		SP	BC	TAR	HB	PaR	WR	PoR	PS	RR	JR
Aat−2	n	176	186	180	88	180	180	112	178	166	114
	117	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	109	0.006	0.000	0.006	0.000	0.000	0.000	0.000	0.006	0.012	0.009
	100	0.761	0.715	0.761	0.773	0.778	0.789	0.723	0.787	0.747	0.711
	89	0.233	0.285	0.228	0.227	0.222	0.211	0.277	0.208	0.241	0.281
	H	0.364	0.462	0.400	0.364	0.267	0.374	0.446	0.337	0.410	0.456
	D	−0.006	0.135	0.084	0.039	−0.228	0.133	0.116	−0.003	0.043	0.097
Est−1	n	180	178	172	182	144	178	182	182	184	176
	102	0.000	0.006	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000
	100	0.651	0.517	0.384	0.440	0.625	0.590	0.604	0.429	0.424	0.358
	98	0.108	0.107	0.238	0.159	0.104	0.163	0.132	0.176	0.130	0.250
	96	0.145	0.107	0.099	0.110	0.111	0.129	0.148	0.203	0.163	0.108
	94	0.086	0.197	0.203	0.192	0.153	0.112	0.088	0.187	0.223	0.239
	92	0.011	0.067	0.076	0.099	0.007	0.006	0.022	0.005	0.060	0.045
	H	0.699	0.865	0.837	0.890	0.722	0.742	0.736	0.912	0.837	0.852
	D	0.305	0.298	0.129	0.231	0.284	0.243	0.252	0.287	0.157	0.154
Est−3	n	174	180	182	176	120	174	174	90	166	182
	108	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	104	0.000	0.233	0.011	0.000	0.000	0.006	0.011	0.144	0.006	0.000
	100	0.443	0.456	0.423	0.244	0.358	0.368	0.345	0.356	0.331	0.478
	96	0.477	0.256	0.495	0.665	0.525	0.603	0.563	0.467	0.578	0.451
	92	0.080	0.044	0.071	0.091	0.117	0.023	0.075	0.033	0.084	0.071
	88	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000
	H	0.448	0.600	0.484	0.409	0.500	0.460	0.545	0.556	0.386	0.446
	D	−0.204	−0.104	−0.154	−0.165	−0.143	−0.080	−0.022	−0.123	−0.297	−0.015
Idh−1	n	180	186	182	184	180	180	182	182	184	184
	98	0.000	0.011	0.005	0.011	0.017	0.006	0.000	0.000	0.005	0.000
	96	0.978	0.984	0.978	0.967	0.961	0.967	0.989	0.978	0.973	1.000
	94	0.017	0.005	0.005	0.016	0.011	0.028	0.011	0.011	0.016	0.000
	92	0.006	0.000	0.011	0.005	0.011	0.000	0.000	0.011	0.005	0.000
	H	0.044	0.032	0.044	0.065	0.078	0.067	0.022	0.044	0.054	0.000
	D	0.018	0.012	0.015	0.023	0.027	0.030	0.010	0.017	0.020	0.000
Idh−2	n	180	186	182	184	180	180	182	182	184	184
	100	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.005
	98	1.000	1.000	0.995	0.989	0.994	0.994	1.000	0.989	0.995	0.957
	96	0.000	0.000	0.000	0.011	0.006	0.006	0.000	0.011	0.005	0.038
	H	0.000	0.000	0.011	0.022	0.011	0.011	0.000	0.022	0.011	0.087
	D	0.000	0.000	0.005	0.011	0.010	0.010	0.000	0.010	0.005	0.040
Lap−1	n	180	182	182	184	174	164	174	182	184	184
	104	0.050	0.088	0.022	0.033	0.052	0.030	0.029	0.011	0.027	0.027
	102	0.528	0.648	0.538	0.592	0.649	0.512	0.523	0.549	0.533	0.522
	100	0.272	0.181	0.308	0.266	0.195	0.348	0.305	0.269	0.288	0.272
	98	0.100	0.071	0.115	0.098	0.092	0.098	0.098	0.148	0.125	0.152
	96	0.044	0.011	0.011	0.011	0.011	0.012	0.046	0.022	0.027	0.027
	94	0.006	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	H	0.589	0.429	0.648	0.598	0.425	0.573	0.690	0.484	0.620	0.685
	D	−0.069	−0.198	0.079	0.052	−0.196	−0.054	0.109	−0.199	0.005	0.088
Lap−2	n	180	182	180	184	178	180	182	170	182	178
	98	0.000	0.011	0.000	0.011	0.011	0.000	0.000	0.000	0.005	0.011
	96	0.067	0.077	0.117	0.082	0.129	0.056	0.066	0.071	0.071	0.096
	94	0.811	0.747	0.717	0.717	0.736	0.778	0.797	0.718	0.747	0.803
	92	0.122	0.159	0.167	0.185	0.124	0.167	0.137	0.206	0.176	0.090
	90	0.000	0.005	0.000	0.005	0.000	0.000	0.000	0.006	0.000	0.000
	H	0.311	0.319	0.411	0.370	0.360	0.333	0.385	0.329	0.407	0.348
	D	−0.034	−0.223	−0.077	−0.169	−0.156	−0.085	0.125	−0.247	0.003	0.033

TABLE 2. Genic variation of the American oyster *Crassostrea virginica* among oyster bars from Chesapeake Bay (continued).

Locus	Allele[2] (RM)	Chesapeake Bay Oyster Bars[1]									
		SP	BC	TAR	HB	PaR	WR	PoR	PS	RR	JR
Mdh−1	n	180	186	182	184	180	180	182	182	184	184
	104	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000
	100	1.000	1.000	1.000	0.995	0.989	0.983	0.995	1.000	0.989	0.995
	96	0.000	0.000	0.000	0.005	0.011	0.017	0.000	0.000	0.005	0.005
	92	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000
	H	0.000	0.000	0.000	0.011	0.022	0.033	0.011	0.000	0.022	0.011
	D	0.000	0.000	0.000	0.005	0.010	0.017	0.010	0.000	0.009	0.005
Mdh−2	n	180	186	182	184	180	180	182	182	184	184
	103	0.006	0.005	0.000	0.000	0.006	0.000	0.005	0.011	0.005	0.000
	98	0.994	0.984	0.989	0.995	0.989	0.983	0.984	0.984	0.989	0.995
	93	0.000	0.005	0.011	0.005	0.006	0.017	0.011	0.005	0.005	0.005
	88	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	H	0.011	0.032	0.022	0.011	0.022	0.033	0.033	0.033	0.022	0.011
	D	0.010	0.008	0.010	0.005	0.010	0.017	0.014	0.013	0.009	0.005
Mpi−2	n	98	156	176	150	162	176	182	170	174	176
	96	0.204	0.038	0.102	0.040	0.253	0.045	0.027	0.018	0.040	0.023
	92	0.194	0.096	0.398	0.440	0.272	0.227	0.330	0.259	0.374	0.392
	88	0.490	0.462	0.341	0.333	0.352	0.477	0.484	0.518	0.408	0.369
	84	0.112	0.308	0.108	0.173	0.093	0.148	0.132	0.147	0.132	0.165
	80	0.000	0.096	0.045	0.013	0.031	0.074	0.027	0.024	0.046	0.034
	76	0.000	0.000	0.006	0.000	0.000	0.028	0.000	0.035	0.000	0.017
	H	0.778	0.821	0.852	0.893	0.815	0.705	0.725	0.741	0.828	0.852
	D	0.162	0.221	0.216	0.345	0.119	0.020	0.136	0.156	0.231	0.252
6Pgdh	n	180	186	182	184	178	180	182	182	184	178
	109	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011
	106	0.022	0.027	0.016	0.011	0.051	0.017	0.000	0.011	0.016	0.022
	103	0.872	0.844	0.951	0.864	0.876	0.889	0.885	0.962	0.891	0.916
	100	0.106	0.129	0.033	0.125	0.073	0.094	0.115	0.027	0.092	0.051
	H	0.211	0.269	0.077	0.228	0.191	0.200	0.165	0.055	0.217	0.157
	D	−0.073	−0.004	−0.186	−0.041	−0.146	−0.006	−0.194	−0.265	0.105	−0.007
Pgi	n	180	186	182	182	178	180	182	182	184	184
	114	0.006	0.000	0.000	0.005	0.006	0.000	0.000	0.005	0.000	0.000
	110	0.022	0.022	0.044	0.055	0.028	0.039	0.049	0.044	0.054	0.016
	106	0.672	0.747	0.703	0.643	0.702	0.656	0.659	0.703	0.674	0.739
	100	0.289	0.210	0.242	0.297	0.258	0.300	0.286	0.236	0.261	0.239
	94	0.011	0.022	0.005	0.000	0.006	0.006	0.005	0.011	0.011	0.005
	90	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	H	0.444	0.387	0.505	0.473	0.449	0.467	0.484	0.473	0.522	0.370
	D	−0.043	−0.024	−0.089	−0.047	0.023	−0.026	0.005	0.057	0.098	−0.066
Pgm−1	n	178	180	182	184	180	180	182	182	184	184
	108	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
	106	0.034	0.056	0.022	0.005	0.022	0.039	0.049	0.038	0.049	0.038
	104	0.320	0.289	0.198	0.255	0.250	0.328	0.253	0.209	0.152	0.234
	102	0.500	0.567	0.676	0.630	0.644	0.550	0.593	0.698	0.696	0.620
	100	0.107	0.061	0.093	0.087	0.067	0.072	0.099	0.049	0.071	0.087
	98	0.028	0.028	0.011	0.022	0.017	0.011	0.005	0.005	0.033	0.022
	H	0.674	0.633	0.462	0.543	0.444	0.600	0.582	0.484	0.522	0.478
	D	0.064	0.078	−0.067	0.027	−0.140	0.029	0.013	0.038	0.076	−0.134
Pgm−2	n	180	178	90	184	180	180	182	90	184	92
	104	0.083	0.152	0.044	0.043	0.194	0.050	0.093	0.022	0.071	0.043
	100	0.883	0.815	0.944	0.886	0.772	0.811	0.824	0.933	0.875	0.924
	96	0.033	0.034	0.011	0.071	0.033	0.139	0.082	0.044	0.054	0.033
	H	0.200	0.281	0.111	0.228	0.344	0.311	0.308	0.133	0.250	0.130
	D	−0.048	−0.101	0.042	0.094	−0.055	−0.028	0.007	0.053	0.106	−0.091

TABLE 2. Genic variation of the American oyster *Crassostrea virginica* among oyster bars from Chesapeake Bay (concluded).

Locus	Allele[2] (RM)	Chesapeake Bay Oyster Bars[1]									
		SP	BC	TAR	HB	PaR	WR	PoR	PS	RR	JR
Sdh	n	--	--	92	148	--	178	182	88	182	88
	110	--	--	0.043	0.061	--	0.051	0.027	0.034	0.038	0.034
	105	--	--	0.891	0.858	--	0.854	0.896	0.898	0.901	0.909
	100	--	--	0.065	0.081	--	0.096	0.077	0.068	0.060	0.057
	H	--	--	0.217	0.284	--	0.247	0.187	0.159	0.198	0.182
	D	--	--	0.087	0.117	--	−0.048	−0.023	−0.157	0.084	0.081
Number of loci studied		29	31	30	32	31	32	32	30	32	32
Mean number of genes sampled per locus		177 ± 15	181 ± 11	175 ± 23	175 ± 24	169 ± 23	173 ± 26	176 ± 17	171 ± 28	182 ± 5	173 ± 28
Polymorphic loci/population[3]		0.483	0.483	0.517	0.552	0.552	0.552	0.517	0.517	0.552	0.517
Heterozygous loci per individual[3]:											
Observed		0.214 ±0.006	0.216 ±0.006	0.215 ±0.006	0.230 ±0.006	0.195 ±0.006	0.216 ±0.006	0.222 ±0.006	0.196 ±0.006	0.227 ±0.006	0.218 ±0.006
Expected		0.209 ±0.006	0.212 ±0.006	0.204 ±0.006	0.209 ±0.006	0.202 ±0.006	0.209 ±0.006	0.210 ±0.006	0.194 ±0.006	0.211 ±0.006	0.207 ±0.006

[1] Oyster bars: Swan Point (SP), Herring Bay (HB), Broad Creek (BC), Tred Avon River (TAR), Patuxent River (PaR), Wicomico River (WR), Potomac River (PoR), Pocomoke Sound (PS), Rappahanock River (RR), and James River (JR).

[2] Allele: RM = relative allelic mobility on the gel

                       n = number of genes sampled per locus

                       H = observed heterozygosity

                       D = $[(H_O - H_e)/H_e]$, where H_O is the observed number of heterozygotes and H_e is the Hardy-Weinberg expected number of heterozygotes.

[3] Based on 29 structural loci (*AcP*−1, *AcP*−3, and *Sdh* could not be resolved for all collecting localities).

genetic variation from the ten naturally occurring oyster bars (Table 2) indicates that the proportion of polymorphic loci (i.e., an estimate of the number of loci which exhibit genic variation with the common allele [p] $\leqslant 0.99$ from a random sample of structural loci in the population) ranges from 0.483 to 0.552 among the ten collecting localities. The observed heterozygosity (i.e., the proportion of genic variation per individual) ranged from 0.195 to 0.230 among the ten demes while the expected heterozygosities ranged from 0.194 to 0.211.

In Table 2, the allele frequencies for the polymorphic loci have been tabulated with respect to the geographic spatial distribution of the oyster bars. No macrogeographic cline is evident in any allele frequency across sampling localities over the latitudinal distribution of *Crassostrea virginica* in Chesapeake Bay. Also, little genetic differentiation exists among the ten sampling localities based upon estimates of genetic similarities and distances (Nei 1972). That is, the genetic similarity among oyster bars ranged from 0.985 to 0.998 while the genetic distances ranged from 0.002 to 0.015. A Pearson chi-square statistic was used to test the null hypothesis that the allele frequencies are homogeneous among all oyster bars. This chi-square analysis of the inter-oyster bar allelic contingency revealed heterogeneity for 12 of the 18 polymorphic loci which indicated among-locus discordance between oyster bars

for two thirds of the polymorphic loci sampled in this study (Table 3).

Environmental versus Genetic Variation among Oyster Bars

In spite of a moderate level of environmental variation and a great diversity in strength of recruitment among oyster bars (cf. Table 1), there appears to be little genetic differentiation among oyster bars in Chesapeake Bay based on estimates of genetic distance, similarity, and variation (above; Table 2). Principle component and stepwise multivariate discriminant analyses were employed to identify any correlation between environmental variation and genetic differentiation. The variables used were water depth, temperature, salinity, and recruitment from Table 1, and deme genic polymorphism and observed individual heterozygosity from Table 2. The results of three principle component plots involving principle components one, two and three indicated that the ten oyster bars were diffused throughout each plot with no clustering of collected localities. When a stepwise multivariate discriminant analysis was conducted between those localities from the upper (Swan Point, Herring Bay, Broad Creek, and Tred Avon River) and those from lower Chesapeake Bay (Patuxent River, Potomac River, Wicomico River, Pocomoke Sound, Rappahanock River, and James River), no discriminating variables were found.

TABLE 3.

Inter-oyster bar allelic contingency tests for 18 polymorphic
loci in the American oyster *Crassostrea virginica* in
Chesapeake Bay.

Locus	Number of Alleles*	Chi-square	d.f.	Probability
$Ap-1$	4	59.327	27	<0.001
$Adk-1$	4	71.750	27	<0.001
$Aat-2$	2	6.353	9	>0.700
$AcP-3$	3	124.720	12	<0.001
$Est-1$	4	133.374	27	<0.001
$Est-3$	3	89.699	18	<0.001
$Idh-1$	2	9.886	9	>0.300
$Idh-2$	2	31.449	9	<0.001
$Lap-1$	5	66.789	36	<0.001
$Lap-2$	3	29.456	18	<0.050
$Mdh-1$	2	10.179	9	>0.300
$Mdh-2$	2	3.328	9	>0.900
$Mpi-2$	5	257.071	36	<0.001
$6Pgdh$	3	44.815	18	<0.001
Pgi	3	16.078	18	>0.500
$Pgm-1$	3	192.985	18	<0.001
$Pgm-2$	3	86.173	18	<0.001
Sdh	3	5.447	12	>0.900
Total		1238.879	330	<0.001

*Rare alleles have been pooled with the next most common allele
for statistical reasons.

F_{st} *Analysis of Allele Frequencies*

Although there were no apparent correlations of environ-
mental or geographical variables with levels of genetic
variation, among-locus discordance existed with respect to
spatial variation among oyster bars as indicated by the
contingency chi-square analysis of the polymorphic loci.
This suggested several possibilities: (1) differential selection
pressure for some alleles at these polymorphic loci in
response to the local environmental conditions of each
collecting locality, (2) a hierarchical relationship among
oyster bars, or (3) structuring of the dispersal pattern of
planktonic oyster larvae among the collecting localities in
Chesapeake Bay. A widely used method of revealing genic
heterogeneity between sampling areas is the use of the
standardized variance in allele frequencies, F_{st} (Wright
1940, 1969, 1978; Cavalli-Sforza 1966; Neel and Ward
1972). F_{st} estimates tend to be uniform for different
alleles when inbreeding, sample variation (genetic drift),
and random migration are occurring within a species. Con-
versely, natural selection operating independently on each
allele at a locus could reflect a heterogeneous array of F_{st}
values among different alleles. That is, for alleles under
differential selection, the variance in allele frequency, as
well as the F_{st} estimate, would be large. If there is a
balancing selection, the variance in allele frequency among
collecting localities would be small, as would the F_{st}
values. A heterogeneity in F_{st} values can also occur when a
hierarchical relationship exists among collecting localities,
or when migration is nonrandom and displays some pattern.

Table 4 gives the F_{st} values for 41 alleles together with
the number of oyster demes over which they have been
estimated. Any allele with a mean allele frequency of $(\bar{p}) \geqslant$
0.05 among oyster bars was analyzed. These data illustrated
a diversity of F_{st} values for these alleles. The mean F_{st}
value was 0.0161 and the variance $S^2_{F_{st}}$ was 0.000194.

The F_{st} statistic is related to the contingency chi-square
statistic used to test for heterogeneity between demes in
allele frequency estimates. Following the procedures of
Snedecor and Irwin (1933), this relationship can be
expressed as

$$\chi^2 = 2NF_{st},$$

where N is the total sample size over all collecting localities.
In these circumstances F_{st} is a simple function of the chi-
square statistic, with the significance of the chi-square
statistic. Consequently, when the chi-square values were
determined for the 41 F_{st} values, 23 alleles were found to
be statistically significant, indicating heterogeneity for
more than one half of the alleles studied among oyster bars
in Chesapeake Bay (Table 4).

A further examination was made by F_{st} statistics in
testing for spatial heterogeneity among the oyster bars. The
test involved the goodness of fit of the observed distribu-
tion of F_{st} values to a theoretical chi-square distribution
(based on ten oyster bars) with 9 degrees of freedom
(Lewontin and Krakauer 1973). Table 5 compares the
observed distribution of the 41 F_{st} values in Table 4 with
chi-square distributions having 1, 2, 3, 4 and 9 degrees of
freedom. Classes were constructed to be one half of the
standard deviation of the mean F_{st} value. The theoretical
chi-square distribution with 9 degrees of freedom centers
on the observed mean F_{st} of 0.0161, while the other chi-
square distributions with 1 to 4 degrees of freedom were
not altered. The test for the goodness of fit between the
observed and the theoretical distributions gave a $\chi^2 = 27.22$
with 8 degrees of freedom corresponding to $P < 0.001$,
so the observed and theoretical chi-square distributions are
significantly different. A test for the goodness of fit between
the observed F_{st} distribution and a theoretical F_{st} distribu-
tion with fewer degrees of freedom provides better results
(Table 5). For example, the best fit occurs when 3 degrees
of freedom are selected as a mean for the theoretical chi-
square distribution. This indicates that the observed F_{st}
distribution of the 41 alleles compared among ten oyster
bars can best be explained if the ten oyster bars were con-
tained within four subpopulations from Chesapeake Bay.

Another test of heterogeneity is the comparison of the
observed variance of F_{st} with the theoretical variance as
described by Lewontin and Krakauer (1973). The theoretical
variance of F_{st} is given by the expression

TABLE 4.

F_{st} values for different allelic distributions among ten oyster populations of *Crassostrea virginica* from Chesapeake Bay.

Locus	Allele	n*	F_{st}†	Chi-square‡	Probability	Significant
Ap–1	100	10	0.00869	15.781	>0.05	No
	97		0.00635	11.532	>0.20	No
	94		0.00581	10.551	>0.20	No
	91		0.01340	24.334	<0.01	Yes
Acp–3	110	7	0.06102	62.851	<0.001	Yes
	108		0.02095	21.579	<0.01	Yes
	105		0.03449	35.525	<0.001	Yes
Adk–t	100	10	0.01275	23.129	<0.05	Yes
	98		0.00583	10.576	>0.30	No
	96		0.01813	32.888	<0.001	Yes
Aat–2	100	10	0.00421	6.568	>0.50	No
	89		0.00421	6.568	>0.50	No
Est–1	100	10	0.04227	74.311	<0.001	Yes
	98		0.01864	32.769	<0.001	Yes
	96		0.00837	14.714	>0.05	No
	94		0.01973	31.923	<0.001	Yes
Est–3	100	10	0.01888	30.548	<0.001	Yes
	96		0.04459	72.147	<0.001	Yes
Idh–1	96	10	0.00544	9.923	>0.30	No
Lap–t	102	10	0.00980	17.542	<0.05	Yes
	100		0.01150	20.585	<0.02	Yes
	98		0.00596	10.668	>0.20	No
Lap–2	96	10	0.00662	11.135	>0.20	No
	94		0.00676	12.141	>0.20	No
	92		0.00834	14.979	>0.05	No
Mpi–2	92	10	0.04963	80.401	<0.001	Yes
	88		0.01833	29.695	<0.001	Yes
	84		0.02547	41.261	<0.001	Yes
6Pgdh	103	10	0.01346	24.443	<0.01	Yes
	100		0.01594	28.947	<0.001	Yes
Pgi	106	10	0.00516	9.391	>0.30	No
	100		0.00430	7.826	>0.50	No
Pgm–1	104	10	0.01434	26.041	<0.01	Yes
	102		0.01628	29.564	<0.001	Yes
	100		0.00409	7.427	>0.50	No
Pgm–2	104	10	0.03436	52.914	<0.001	Yes
	100		0.02604	40.102	<0.001	Yes
	96		0.02233	34.388	<0.001	Yes
Sdh	110	7	0.00289	2.769	>0.95	No
	105		0.00401	3.842	>υ.90	No
	100		0.00239	2.290	>0.98	No

mean F_{st} = 0.0161   variance $S^2_{F_{st}}$ = 0.000194

*n = number of oyster bars for each F_{st}.

†F_{st} = "effective" inbreeding coefficient.

‡$\chi^2 = 2NF_{st}$ with (n − 1) degrees of freedom.

TABLE 5.

Comparison of the observed distribution of $\hat{F}_{st}$ values of Table 4 with chi-square expected distributions having means of 1, 2, 3, 4, and 9 degrees of freedom.

$\hat{F}_{st}$	Observed	Expected Degrees of Freedom				
		1	2	3	4	9*
<0.0070	15	21.76	16.26	10.95	6.56	5.06
0.0071 – 0.0140	8	9.35	9.86	9.39	7.96	7.68
0.0141 – 0.0210	9	4.59	5.97	6.97	7.25	8.40
0.0211 – 0.0280	3	2.43	3.62	4.88	5.85	7.11
0.0281 – 0.0350	2	1.35	2.20	3.28	4.45	5.12
0.0351 – 0.0420	0	0.74	t.34	2.21	3.24	3.31
0.0421 – 0.0490	2	0.45	0.80	1.44	2.28	1.98
0.0491 – 0.0560	1	0.29	0.48	0.94	1.59	1.12
0.0561 – 0.0630	1	0.04	0.49	0.94	1.80	1.21
Total	41	41.00	41.00	41.00	41.00	41.00
χ^2		11.03	6.26	5.95	17.87	27.22
df		5	6	7	8	8
Probability		>0.05	>0.30	>0.50	<0.05	<0.01

*corrected for the observed mean F_{st}.

$$\sigma^2 = K\bar{F}_{st}/(n − 1),$$

where K = 2 for an underlying binomial distribution of p (the relative allele frequency). When this formula is applied to the data of Table 4,

$$\sigma^2 = 0.000058.$$

Whether or not the observed variance $S^2_{F_{st}} = 0.000194$ is significantly larger than the theoretical variance was tested by the ratio $S^2_{F_{st}}/\sigma^2 = 3.368$ which is distributed as χ^2/df. To compensate for the multiple allelic loci, it was necessary to remove 1 degree of freedom for each multiple allelic loci (Lewontin and Krakauer 1973). The number of degrees of freedom then became 41 − 14 = 27 and the probability of the χ^2/df ratio was P < 0.001, which indicates a significant difference. If the assumption is made that the observed F_{st} distribution can be best explained by assuming four subpopulations in Chesapeake Bay instead of the actual ten oyster bars studied, the σ^2 becomes 0.000173. Whether the observed variance is significantly larger was again tested by the ratio

$$S^2_{F_{st}}/\sigma^2 = 1.121.$$

The probability of the χ^2/df ratio was p > 0.25, resulting in no significant heterogeneity.

The $S^2_{F_{st}}/\sigma^2$ ratio can be inflated by higher migration rates among certain groups of subpopulations, by mutation and special patterns of migration (Nei and Maruyama 1975), as well as by hierarchical relationships among populations

(Robertson 1975). It is likely that higher migration rates exist among neighboring oyster bars than among distant oyster bars. Consequently, the partitioning of the ten oyster bars in this study into four subpopulations greatly reduces the $S^2_{F_{st}}/\sigma^2$ ratio. The difference between the $S^2_{F_{st}}/\sigma^2$ ratios, when 9 and 3 degrees of freedom were used, indicated how this ratio can be inflated if the assumption is made that the ten collecting localities were contained within a single panmictic oyster population instead of four panmictic subpopulations.

The F_{st} analysis indicates that some genetic structure existed among the resident oyster bars of Chesapeake Bay. Although the F_{st} analysis indicated subpopulational structure, it did not assign the ten oyster bars to their respective group nor did it indicate which structural loci were responsible for the partitioning of the ten bars into four subpopulations. A probable solution to these questions can be obtained with the use of principle component and stepwise multivariate discriminant analyses. Using principle

component analysis, the Chesapeake Bay oyster population was considered as a set and the allele frequencies of the polymorphic loci as the variables measured over the ten sampling localities. Twenty-eight of the most common alleles (i.e., p ≥ 0.05) from the *Ap–1*, *Adk–1*, *Aat–2*, *Est–1*, *Est–3*, *Lap–1*, *Lap–2*, *Mpi–2*, *6Pgdh*, *Pgi*, *Pgm–1*, and *Pgm–2* loci (Table 2) were used in the principle component analysis. The *AcP–3* and *Sdh* loci were not used because they were not represented among all oyster demes. Also, the *Idh–1*, *Idh–2*, *Mdh–1*, and *Mdh–2* loci were not used because these genes represented very little genic variation among demes and would not be of much diagnostic value. The results of this analysis are illustrated in Figure 2, where principle component one is plotted against principle component three. The ten collecting localities can be grouped into four subpopulations as shown by the convex contour lines. The first group from the upper Chesapeake Bay contains the Broad Creek, Patuxent River, and Herring Bay oyster bars. Proceeding down the bay, the
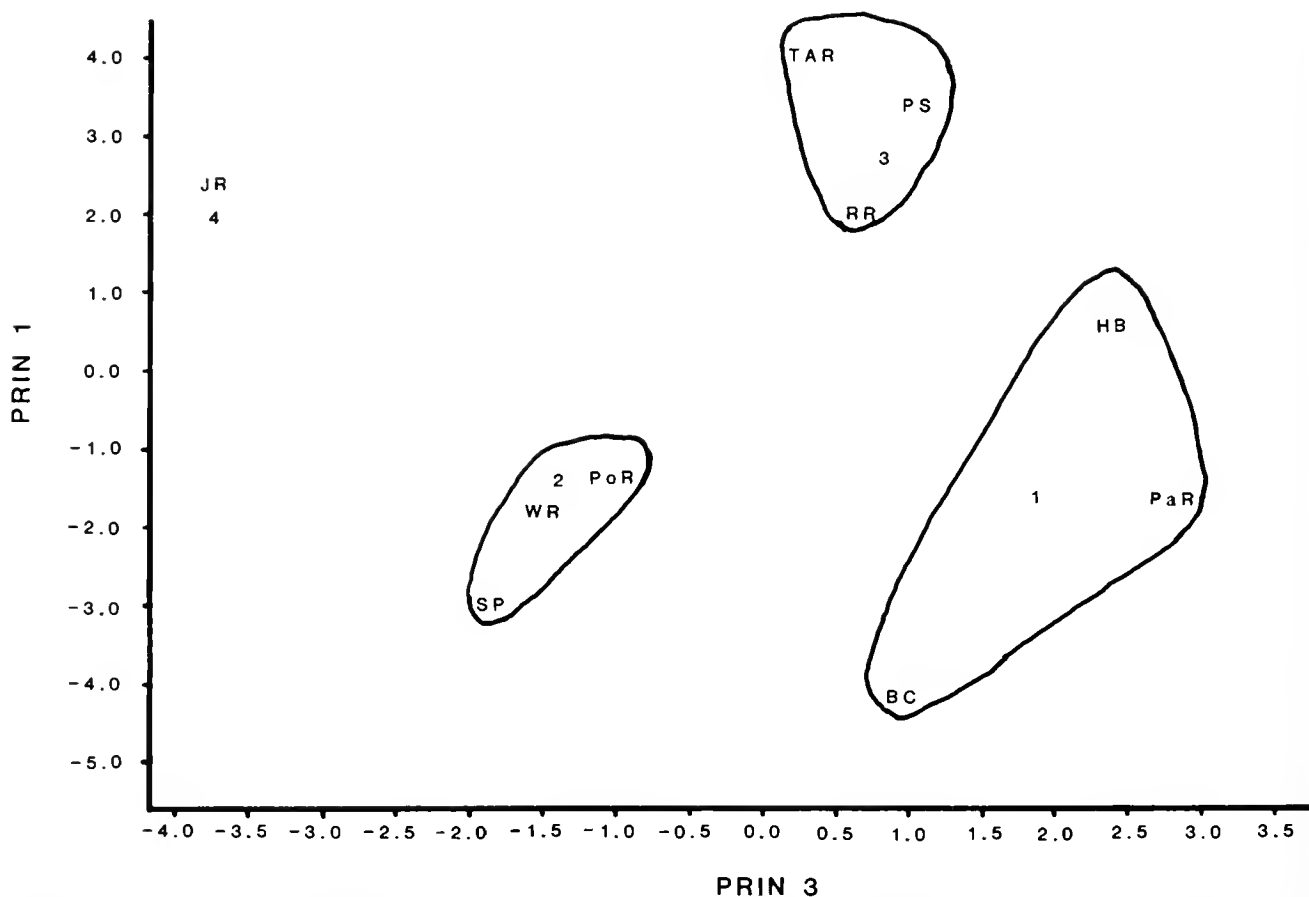
Figure 2. A principle-component analysis involving 28 alleles across 10 oyster bars in Chesapeake Bay. The two-dimensional graph depicts principle components one and three of the analysis. Four different groups from Chesapeake Bay can be recognized. Group one is located in upper Chesapeake Bay and consists of the Broad Creek (BC), Herring Bay (HB), and Patuxent River (PaR) oyster bars. Group two consists of Swan Point (SP), Wicomico River (WR), and Potomac River (PoR) oyster bars. Group three consists of the Tred Avon River (TAR), Pocomoke Sound (PS), and Rappahanock River (RR) oyster bars. Group four would contain the James River (JR) oyster bar. The contour lines are drawn as a visual aid.

second group contains the Swan Point, Wicomico River, and Potomac River oyster bars. The third group encompasses the Tred Avon River, Pocomoke Sound, and Rappahanock River oyster bars. The James River collecting locality appears to be independent of all other groups. The plots of principle components one on two and two on three provided similar results. The separation of the ten oyster bars into four different groups within Chesapeake Bay supports the F_{st} analysis; however, it does not define which alleles of the 12 polymorphic loci are diagnostic in partitioning the ten oyster bars into four subpopulations.

An examination of allelic frequencies for the 18 polymorphic loci indicates that no single locus is diagnostic for partitioning the oyster bars into subpopulations, yet there are discrete allele frequency differences among the ten oyster bars. Using stepwise multivariate discriminant analysis,

the information at these loci was combined to maximize the diagnostic powers. Figure 3 shows the genetic differentiation among nine oyster bars based on the first two canonical variables of the discriminant analysis. The James River oyster bar was excluded from the analysis because it could not be grouped by principle components with any other oyster bar. The $Est-1^{100}$, $Lap-1^{102}$, Pgi^{106}, and $Pgm-1^{104}$ allele frequencies were used in combination by the analysis to partition the remaining oyster bars into three subpopulations.

DISCUSSION

The long planktonic larval development of *Crassostrea virginica* has apparently been beneficial for the longevity of this oyster species because it is this stage of development that provides the opportunity for demes to disperse their
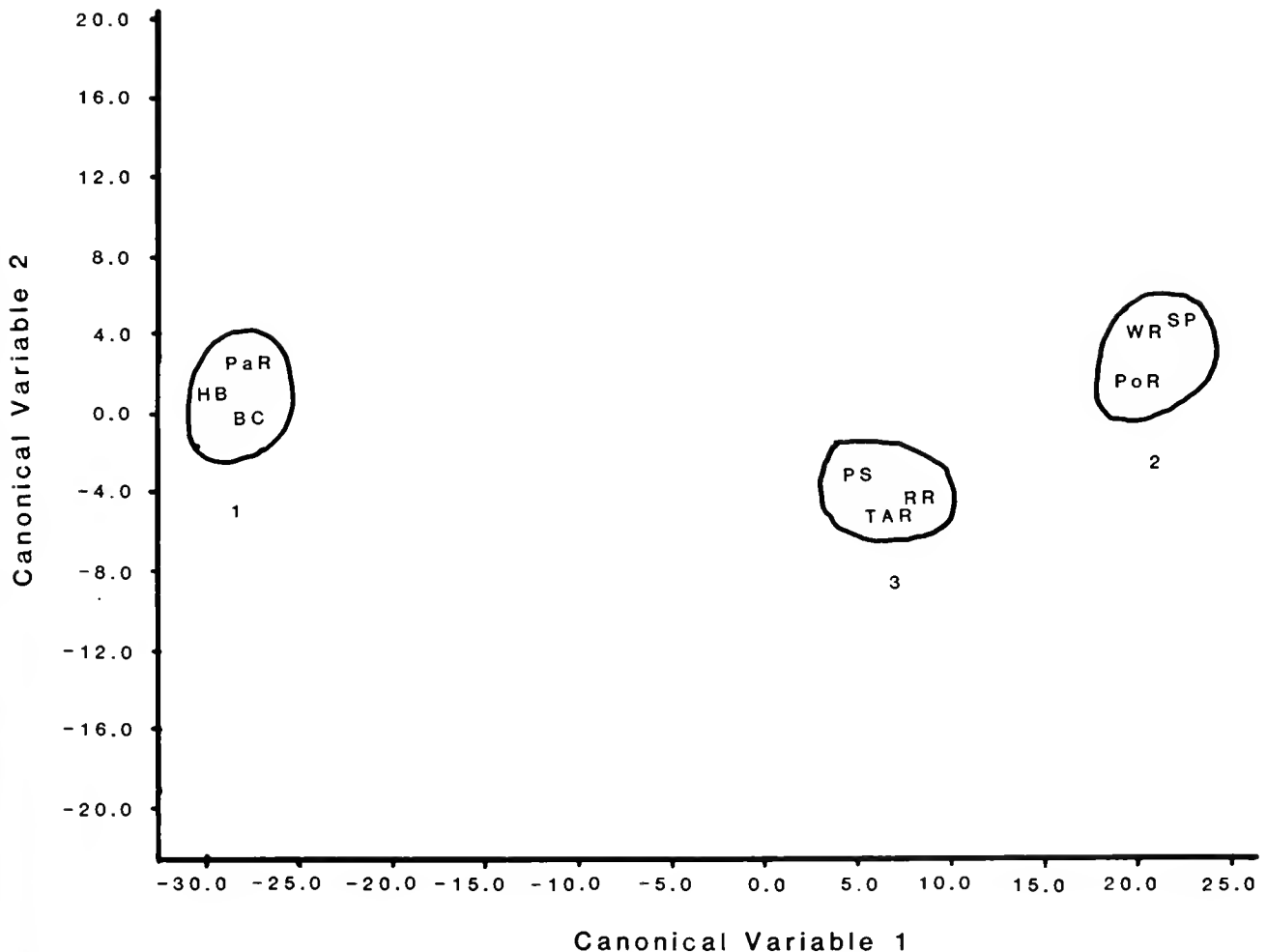
Figure 3. Two-dimensional graph of first two canonical variables from a stepwise multivariant discriminate analysis of 28 alleles across ten oyster bars in Chesapeake Bay. The analysis entered the $Est-1^{100}$, $Lap-1^{102}$, Pgi^{106}, and $Pgm-1^{104}$ alleles in the production of the two canonical variables. Nine oyster bars can be distinctly grouped into three subpopulations. Group one consists of Broad Creek (BC), Herring Bay (HB), and Patuxent River (PaR) oyster bars. Group two consists of Swan Point (SP), Wicomico River (WR), and Potomac River (PoR) oyster bars. Group three consists of Tred Avon River (TAR), Pocomoke Sound (PS), and Rappahanock River (RR) oyster bars. The contour lines are drawn as a visual aid.

zygotes into contiguous populations. As a consequence of this dispersing ability, the fossil record indicates that ancient populations of *C. virginica* apparently had relocated along the Atlantic coast with respect to changing environmental conditions (Merrill et al. 1965). The apparently high levels of gene flow caused by large demes, high individual fecundities, and long planktonic development should be in part responsible for maintaining the relatively high level of genetic variation within this species (Table 2). These levels of genetic variation coincide well with those found in other invertebrates (Lewontin 1974, Powell 1975, Selander 1976). The genetic similarities between oyster bars in Chesapeake Bay are consistent with levels of genetic similarity reported for other intraspecific studies of invertebrates (Ayala et al. 1974, 1975; Hedgecock et al. 1976; Tracey et al. 1975) as well as for other geographical populations of *C. virginica* along the Atlantic coast (Buroker 1983).

In spite of local environmental differences between the ten collecting localities (Table 1), there appears to be no overall genetic differentiation for the 32 loci studied among the oyster bars. When the genetic variation among oyster bars was statistically analyzed, however, gene diversity was found and some structure to the oyster demes in Chesapeake Bay was noted. The use of Wright's (1940, 1969, 1978) inbreeding coefficient and principle component analysis indicated at least four subpopulations of oysters in the bay. The principle component analysis of the allele frequency data produced the best possible grouping arrangement of the ten oyster bars that were examined in this study. When a comparison was made between sampling sites (Figure 1) and their grouping (Figure 2), it became apparent that the common factor which united the oyster bars within a group was their close geographical proximity. For example, the northern most group in Chesapeake Bay consisted of oyster bars within the geographical boundaries of Broad Creek, Herring Bay, and Patuxent River. Moving in a southerly direction, the second group consisted of oyster bars within the boundaries of the Wicomico and Potomac rivers. The third group contained those oyster bars that were geographically bounded by Pocomoke Sound and Rappahanock River. The final group consisted of oyster bars in the lower part of the bay including the James River as part of the subpopulation. These four subpopulations are latitudinally distributed in Chesapeake Bay. This may indicate that gene flow among oyster demes was localized within certain regions of the bay.

At least two observations can be made from a comparison of Figures 1 and 2. First, two oyster bars obviously appear out of place. Based on geographic location, the Swan Point oyster bar (group two) and the Tred Avon River oyster bar (group three) would be more appropriately placed in group one. Second, why should subpopulations exist in Chesapeake Bay when there is a long planktonic stage of larval development for this species and good water circulation in the estuary? Because gene flow between demes, which are in close geographical proximity, appears to be a prominent mechanism in accounting for the oyster population structure in the bay, either random events or selection could be invoked to explain the above two observations. Because numbers of adult oysters per deme may run from hundreds of thousands to millions of individuals (Galtsoff 1964), it is unlikely that random events would be responsible for the genetic differentiation found between the Tred Avon River and Broad Creek oyster bars as well as the Swan Point oyster bar and those demes of group one. The alternative hypothesis would be genotypic adaptation of new recruits to the local environmental conditions of each oyster bar. For example, from the stepwise multivariate discriminant analysis (Figure 3), it is evident that allelic variance of $Est-1^{100}$, $Lap-1^{102}$, Pgi^{106}, and $Pgm-1^{104}$ is minimial within each group and is greatest between subpopulations. Evidence for microgeographical selection of allozyme genotypes in varied environments has been presented for some marine bivalves (Koehn and Mitton 1972; Koehn et al. 1973, 1976, 1980; Levinton 1973; Boyer 1974). Consequently, the microgeographic adaptation of genotypes among Tred Avon River oysters to their ambient environment might concide with that found for oysters within group three instead of group one. The same argument would place the Swan Point bar in group two instead of group one. Obviously this results in a migration-selection model to explain the genetic differentiation found between sampling localities. When the balance within the model is heavily shifted in favor of selection of genotypes to local environmental conditions, the structuring of subpopulations would be negated (which appears to be the situation for Tred Avon River and Swan Point oyster bars).

On a macrogeographical scale the migration-selection model can be used to explain the latitudinal partitioning of oyster subpopulations in Chesapeake Bay. If there was no opposing evolutionary force to counterbalance the effect of gene flow, the bay would consist of a single panmictic population with no genetic differentiation of groups; however, the F_{st} analysis (Table 4) verifies genetic differentiation among sampling localities when 23 of 41 alleles were found to display significant heterogeneity among the ten oyster bars investigated. Because subpopulations are present that consist of minor genetic differences as revealed by statistical analysis of allele frequencies among oyster demes, it is suggested that a macrogeographical selection gradient occurs latitudinally in the bay. Although the exact components of this gradient cannot be defined, attention can be drawn to some environmental similarities that coincide with the subpopulations. The two most obvious environmental parameters are salinity and water temperature, because both form latitudinal clines within the bay (see Materials and Methods). Also, there is a positive relationship between eigenvector coefficients of the principle

component analysis for oyster spat recruitment, salinity, water depth of the oyster bars, deme genic polymorphism, and observed individual heterozygosity (see Results). It must be assumed that some environmental selective effect existed that counteracted migration to establish a balance among these evolutionary forces (i.e., migration and selection) and was responsible for the partitioning of subpopulations. A possible candidate would be *Haplosporidium nelsoni* (Haskin) (MSX) disease which has a history of periodically reoccurring among oyster populations along the Atlantic coast of North America (Andrews and Wood 1967, Haskin and Ford 1982). In Chesapeake Bay, this disease has at times produced heavy mortality among oyster bar in the high-salinity areas of the lower bay while the disease has had no apparent affect among oysters that inhabit the low-salinity environment of the upper bay.

The occurrence of bivalve subpopulations has been hypothesized in some instances to explain heterozygote deficiencies among allozyme genotypes of *Mytilus californianus* (Conrad) (Tracey et al. 1975), *Mytilus edulis* (Linnaeus) (Boyer 1974), *Tridacna maxima* (Röding) (Ayala et al. 1973), and *Crassostrea virginica* (Zouros et al. 1980). If the allele frequencies from two genetically different sampling localities are pooled and Hardy-Weinberg equilibrium frequencies are estimated as if the sample represented one population, the expected frequencies of heterozygous individuals would be over estimated (i.e., the Wahlund effect). When considering the Wahlund effect, it is important to emphasize that (1) the allele frequencies among demes must be different to be able to detect a significant deficit of heterozygous genotypes, and (2) the effect is uniform over all loci which exhibit genic differentiation among demes. A measure commonly used to detect heterozygote deficiences among allozyme genotypes is the "D" statistic (Koehn et al. 1973) in which a positive value indicates a heterozygote excess and a negative value a heterozygote deficit. This value has been recorded in Table 2 for all polymorphic loci across the ten sampling localities. A predominant deficit of heterozygous genotypes was found for the *Est–3*, *Lap–2*, and *6Pgdh* loci over the ten sampling sites. Zouros et al. (1980) also reported heterozygote deficits for *Est–3* and *Lap–2* among their largest weight classes of *C. virginica* collected from Malpeque Bay, Nova Scotia, Canada. Contrary to the deficiency of heterozygotes, an excess of heterozygote genotypes occurred at the *Adk–1*, *Est–1*, and *Mpi–2* loci across the ten oyster bars. Of these six loci, significant heterogeneity occurred across oyster bars (ref: F_{st} analysis, Table 4) for the *Adk–1*, *Est–1*, *Est–3*, *Mpi–2*, and *6Pgdh* loci. The Wahlund effect may be responsible for the deficit of allozyme heterozygotes

which has been reported among marine bivalves if only two alleles are involved. When three or more alleles are present, it is possible to generate an overall excess of heterozygous genotypes (Li 1969, Milkman 1975, Koehn et al. 1976). The *Est–3*, *Lap–2*, and *6Pgdh* loci generally have two common alleles while the *Adk–1*, *Est–1*, and *Mpi–2* loci have three or more common alleles. Consequently, the Wahlund effect can explain both excesses and deficits of heterozygous genotypes within a collecting locality. Balancing selection has also been used to explain heterozygote deficits in marine bivalves (Koehn and Mitton 1972; Koehn et al. 1973, 1976; Mitton et al. 1973; Boyer 1974) while a heterozygote advantage has been used to explain heterozygote excesses among bivalves (Buroker 1979, Fujio et al. 1979, Zouros et al. 1980).

In conclusion, the levels of genetic variation for *Crassostrea virginica* in Chesapeake Bay coincide well with those found for other geographical populations along the Atlantic coast of North America (Buroker 1983). Although the genetic distances among oyster bars in the bay were small, interdemic heterogeneity was found for 23 of 41 alleles tested. It was by means of this among-locus variation across oyster bars that subpopulations were classified primarily by principle component and discriminant analyses. The subpopulations and among-locus variation across oyster bars are thought to be maintained through a balance between migration and selection. Because this study only draws attention to the possibility of population differentiation among marine bivalves with long planktonic stages of larval development, the findings of this report should be thoroughly tested by investigations which analyze the temporal genetic stability of recruits as compared to resident individuals.

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FEASIBILITY OF MARICULTURE OF THE HARD CLAM
MERCENARIA MERCENARIA (LINNÉ)
IN COASTAL GEORGIA

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ABSTRACT   Caging, baffles, and the utilization of feeder creeks and tent structures were tested as predator controls to determine if mariculture of the hard clam *Mercenaria mercenaria* (Linné) is feasible in coastal waters of Georgia. Clams were planted at densities of 509, 1009, 2018, and 3027 clams m^{-2} in replicate plots within predator-free cages on an intertidal sandflat at Cabbage Island, Wassaw Sound, Georgia. Seed clams grew from a mean shell length (SL) of 6 to 24 mm in 7 months with no observed density effects on survival or growth (ANOVA $\propto$ = 0.05). Seed clams (4,000 of 10-mm SL and 40 of 25-mm SL) were planted in replicate plots (2.25 m^2) of baffles and mud, baffles, mud and tops, baffles and gravel, and baffles and mixed oyster shells. No differences in survival were evident between test treatments for either seed size (ANOVA $\propto$ = 0.05). Seed clams (76 of 30-mm SL and 4,000 of 5-mm SL) were planted on the bottom of a feeder creek in replicate plots of mud, mud plus mixed oyster shells, mud plus tent, and mud with shells and tent. Survival for the 30-mm SL seed clams ranged from 43 to 86% and was <1% in all plots for 5-mm SL seed clams. No differences in percent survival were evident between plots for either size class (ANOVA $\propto$ = 0.05). A plan is presented for hard clam mariculture in the coastal waters of Georgia.

KEY WORDS   Hard clams, *Mercenaria mercenaria*, mariculture, predation, Georgia.

INTRODUCTION

The hard clam *Mercenaria mercenaria* (Linné) represents a new and potentially important supplemental fishery for the state of Georgia. The potential of the fishery is viewed primarily as an off-season fishery for the blue crab (*Callinectes sapidus* [Rathbun]) fishermen in Georgia.

The extent of the hard clam resource in Georgia is unknown. Godwin (1967, 1968) conducted a clam survey of 432 stations in inshore Georgia waters (estuaries and creeks). Clams occurred at 41 stations, primarily in intertidal, higher saline areas with sand-mud or sand-mud-shell substrates. Godwin (1967) reported a maximum clam density of 16 m^{-2} (151 · 100 ft^{-2}) with a mean density of 5 clams m^{-2}, and concluded that, at that time, a commercial hard clam fishery was not feasible.

In more northern U.S. waters, *M. mercenaria* occurs primarily subtidally in sounds or estuaries. In Georgia, however, most clam beds in Wassaw Sound are located intertidally in the headwaters of major creeks, in the small feeder creeks, among live oysters, or among oyster-shell deposits associated with live oyster reefs at densities of up to 100 clams m^{-2} (Walker et al. 1980, Walker and Tenore [in press]). Areas with densities greater than 25 clams m^{-2} are not uncommon in the small feeder creeks and in the headwaters of the major creeks of the higher saline areas of the Sound. These densities are much higher than those reported by Godwin (1967) and could support a small commercial fishery. Though dense, these clam beds are small and are easily overfished. For example, one clam bed of approximately 90-m^2 area which had a mean density of 49 clams m^{-2} occurs in a feeder creek (3 × 61 m) located on a Wassaw

Island, a National Wildlife Refuge. This bed was illegally fished in 1981 and the mean density decreased from 49 to 21 clams m^{-2} within a week (Walker, in preparation). Susceptibility to overfishing may explain the sporadic nature of the hard clam fishery during the past 103 years in Georgia (Walker et al. 1980).

One method of maintaining clam production in Georgia may be through clam mariculture. Clams grow year around in the coastal waters of the southeastern United States (Eldridge et al 1976), and Georgia has vast areas suitable for shellfish culturing. The major problem with clam mariculture in Georgia is predation by blue crabs (Walker et al. 1980) and mud crabs (*Panopeus herbstii* [Say]) (Whetstone and Eversole 1977). Methods for reducing clam predation include fencing, caging, utilizing various types of aggregates (gravels, shell), and baffles (Kraeuter and Castagna 1980, Castagna and Kraeuter 1981). The purpose of this paper is to discuss the feasibility of clam mariculture in the coastal waters of Georgia.

Study Site Location

Wassaw Sound (Figure 1) is an estuarine embayment located in the Georgia Bight (Howard and Frey 1980). Tides are semidiurnal and average 2.4 m amplitude, with spring tides ranging approximately 3.4 m (Hubbard et al. 1979). Water temperatures range from 8 to 30°C (Dörjes 1972) and salinities at the mouth of the Sound range from 20 ppt in the winter to 30 ppt in the summer (Howard and Frey 1980). Sediments range from silty clay to fine sand; interbedded sand-mud is the most prevalent sediment (Howard and Frey 1975).
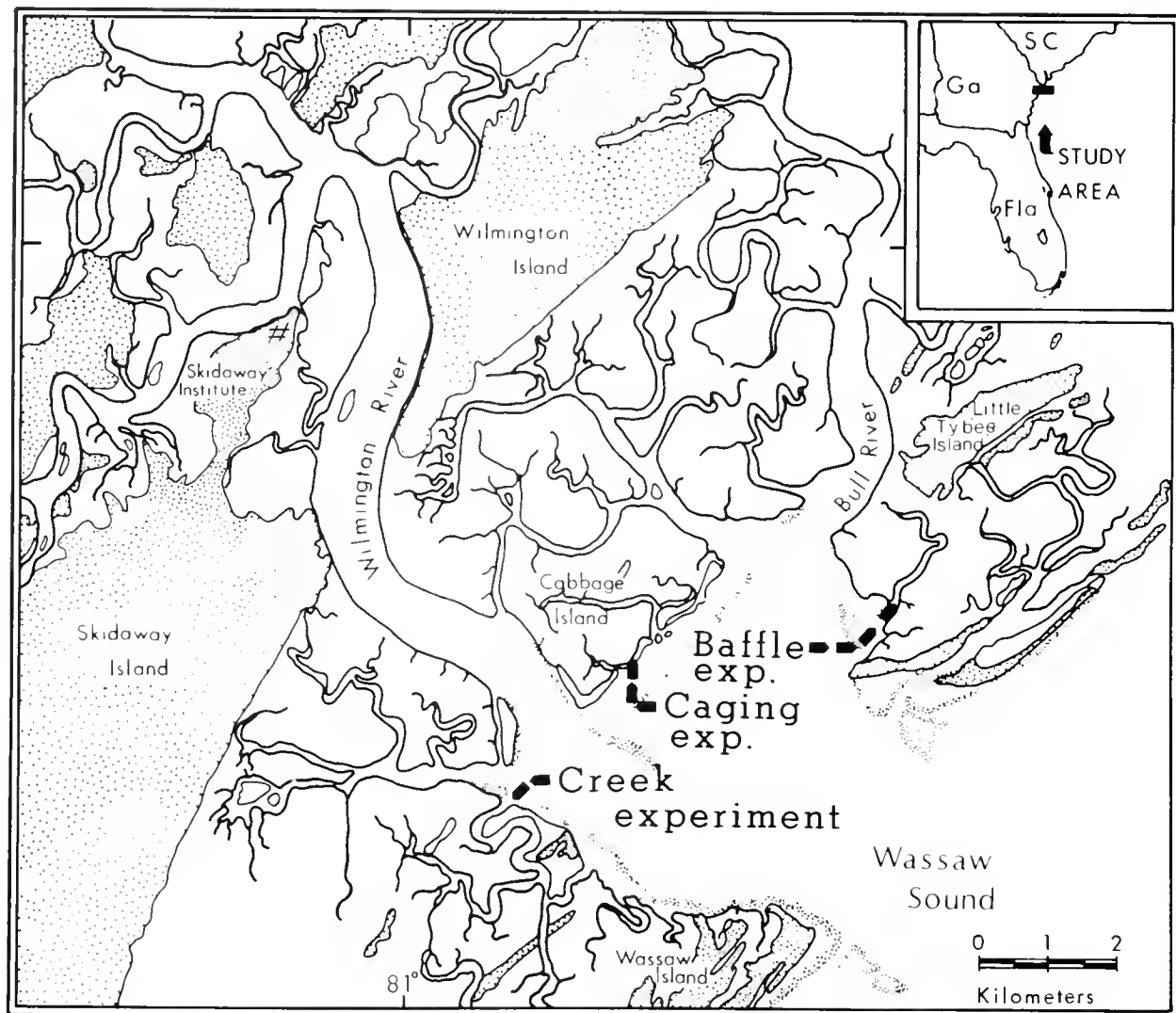
Figure 1. Wassaw Sound showing various experimental study sites.

MATERIALS AND METHODS

Clams were obtained from Aquaculture Research Corporation, Dennis, Massachusetts, in June 1982, and planted and maintained at different densities (509, 1009, 2018, and 3027 m^{-2}) within 1- × 1- × 0.3-m cages constructed of 3-mm mesh Vexar® plastic. The plastic mesh was attached to 1- × 1- × 1-m frames constructed of 13-mm steel reinforcing rods. The resulting structure was buried to a depth of 0.85 m into a sandy sediment on an intertidal flat at Cabbage Island, GA (Figure 1). Cages were sampled monthly to a sediment depth of 10 cm, with sediment, clams and crabs sieved through a 5-mm mesh screen. Clams were counted and a subsample (n = 70) was measured for shell length (anterio-posterior measurement); the clams were then returned to their original plot. Crabs were identified as to species, measured for carapace width, and discarded. Differences in clam growth rates were determined by analysis of covariance (ANCOVA).

In October 1982, 2.25-m^{2} replicate plots of baffles and mud, baffles, mud and tops, baffles and 151 ℓ of mixed oyster shell, and baffles and 151 ℓ of crushed aggregate gravel (No. 57, coarse; mean diameter = 5 cm) were set up on an intertidal mud flat at House Creek (Figure 1). Baffles were constructed of 6-mm mesh Vexar® plastic attached to a 13-mm steel reinforcement rod. Four baffles were buried in the mud at right angles to each other until the Vexar® plastic was 0.15 m deep. Baffles were allowed to stand 2 months before the shell, gravel, or tops were added. After two weeks, 40 seed clams of 2-cm SL (18 m^{-2}) and 400 seed clams of 1-cm SL (178 m^{-2}), each size class identifiable by color codes using Krylon® spray paint, were placed into each plot. Tops constructed of 25-mm mesh Vexar® plastic (i.e., bird netting) were attached to two plots after seeding. Plots were sampled as above in July 1983. The mean survival percentage was determined for each plot and clam size class. The resulting data were examined statistically by analysis of variance (ANOVA).

In October 1982, experimental plots (3.7 × 4.3 m) were established in two mud-bottom feeder creeks located at Wassaw Island (Figure 1). Wild clams were removed by raking. The following replicate plot types were set up: mud bottom, mud bottoms with 151 ℓ of washed oyster shell, mud bottoms with a "tent structure," and mud bottoms with 151 ℓ of shell and a tent structure. Tents were constructed of 13-mm Vexar® plastic which was cut into 3.7 × 4.3-m sections. Along the long sides 13-mm steel reinforcement rods were attached and along the short sides 3.7 m of 13-mm galvanized chain was attached and buried in the substrate. Four, 15-cm diameter styrofoam, crab-trap floats were attached along the midline of the structure. At low tide the structure rested flat on the bottom and floated into a pup-tent form as the tide entered the creek.

Each plot was seeded with 4,000 clams of 0.5 cm SL (251 m^{-2}) and 76 clams of 3.0-cm SL (5 m^{-2}); each size class was color coded using Krylon® spray paint. In addition, four plots, one of each test variable, received 80 of 1-cm SL and 45 of 2-cm SL seed clams. Whole plots were sampled in August by sieving sediments to a depth of 10 cm and clams through a 5-mm mesh screen. The clams were counted and shell lengths were determined using vernier calipers. The numerical data were statistically analyzed by analysis of variance.

RESULTS

No significant differences existed in growth rates (ANCOVA ∝ = 0.05), in final shell length (ANOVA ∝ = 0.05), or in survival per density per month (ANOVA ∝ = 0.05). Clams grew from an initial mean shell length of 6.1 to 23.9 mm (Table 1) from June 1982 to January 1983. Growth rates at each density are given in Figure 2. Instantaneous clam survival was lowest in July (76.5%) but exceeded 99.0% by October (Table 2).

In the baffle experiment, total clam survival was greater for the 2.5-cm seed clams (72%) than for the 1.0-cm clams (23%). No significant differences existed between protective methods (ANOVA ∝ = 0.05) for either the 2.5- or 1.0-cm clams; however, survival percentages per treatment were as follows: (1.0-cm size class) mud, baffles, and top (29%), mud and baffles (26%), shell and baffles (23%), and gravel and baffles (11%); (2.5-cm size class) mud and baffle (88%), shell and baffle (73%), mud, baffle, and top (68%), and gravel and baffle (45%).

In the tidal creek experiments, total clam survival decreased with decrease in clam size as follows: 3 cm (66%) > 2 cm (57%) > 1 cm (40%) > 0.5 cm (0.04%). For the 3-cm size class, no significant differences existed between plots (ANOVA ∝ = 0.05); however, clam survivals per treatment were as follows: shell and tent (86%) > mud and tent (70%) > shell (62%) > mud (43%). For the 5-mm clams, no significant differences existed in clam survival between plots (ANOVA ∝ = 0.05). Mortality of 5-mm clams

exceeded 99% in all plots. For the 2-cm clams, 76% were recovered from shell and tent plots, 64% from mud and tent plots, 53% from shell plots, and 4% from mud plots. For the 1.0 cm clams, 81% were recovered from the shell and tent plot, 73% from the shell plot, 4% from the mud plot and 0% from the mud and tent plot.

DISCUSSION

Mortality reduction is essential to any successful clam mariculture program. The size(s) at which hard clams are no longer preyed upon by different predators are as follows: *Cancer irroratus* Say (15 mm) (MacKenzie 1977), *Urosalpinx cinerea* Say (20 mm) (MacKenzie 1977), *Panopeus herbstii* (35 mm) (Whetstone and Eversole 1981), *Callinectes sapidus* (40 mm) (Arnold 1983), and *Menippe mercenaria* (Say) (70 mm) (Arnold 1983). Whelks of the genus *Busycon* prey on all sizes of clams (Peterson 1982). If unprotected seed clams are planted in the field, they are preyed upon by a host of predators. *Menippe mercenaria* and *Busycon* whelks are capable of preying upon commercial-size clams. Thus, some means of protection is mandatory.

Clam mariculture attempts in the field using various methods of seed protection have had mixed success. Seed clams (10 mm) which were planted in unfenced and fenced plots with 1.8-m high and 13-mm mesh plastic screen in Florida resulted in 100% mortality (Menzel and Sims 1964). Clams ranging from 33- to 44-mm SL that were planted in those plots suffered 100% mortality in the unfenced plots and less than 5 to 18% mortality in fenced plots (Menzel and Sims 1964). Seed clams that were planted in fenced plots in Virginia averaged 94% survival as compared to 8.8% for those in unfenced plots (Kraeuter and Castagna 1980). Field experiments in Virginia, using crushed rocks, pea gravel, crushed oyster shell, or whole oyster shell as protective cover for 0.6 to 20-mm seed clams, resulted in survivals greater than 80% as compared to 15 to 35% survival in unprotected control plots (Castagna 1970); however, in Florida, the survival rate of seed clams (4 to 20 mm) was 10% in plots with pea gravel, 2% in crushed oyster shell, and less than 1% in controls (Menzel et al. 1976). Fenced clam plots in Chesapeake Bay did not increase survival; however, gravel did increase clam survival by 10% for 2 to 17-mm seed clams (Haven and Loesch 1973). Thus, depending upon location and environmental conditions, the use of these protective measures may result in widely varying rates of survival.

Acceptable survival in Georgia (> 70%) resulted for seed clams greater than 20 mm when protected by baffles, baffles and shell, shell and tents, and for seed clams greater than 10 mm when planted in cages. The survival of seed clams in cages is dependent upon the monthly removal of crabs, *Callinectes sapidus* and/or *Panopeus herbstii*, which probably entered cages as metamorphosing juveniles (Figure 3). In similar cages, which were planted earlier at the same site, seed-clam (10 mm) survival in the first year

TABLE 1.

Growth (in mm) of hard clams that were planted at densities of 509, 1009, 2018, and 3027 m^{-2}
on an intertidal sandflat at Cabbage Island, Georgia.

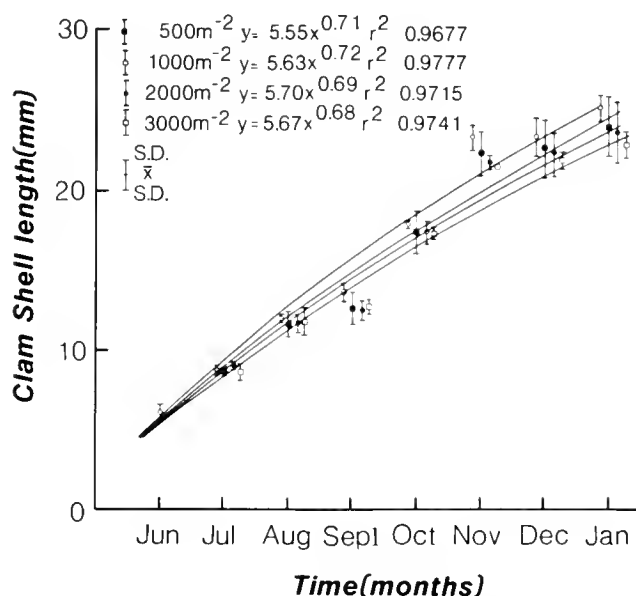| | Densities | | | | | | | |
| | 509 m^{-2} | | 1009 m^{-2} | | 2018 m^{-2} | | 3027 m^{-2} | |
Date	Plot 1	Plot 2	Plot 1	Plot 2	Plot 1	Plot 2	Plot 1	Plot 2
June 1982	6.1	6.1	6.1	6.1	6.1	6.1	6.1	6.1
July 1982	8.5	8.4	8.7	8.8	8.9	9.0	8.2	8.9
August 1982	11.0	12.1	11.9	12.0	12.7	11.3	12.3	11.1
September 1982	13.3	11.9	13.2	14.0	12.0	13.0	12.4	13.0
October 1982	18.3	16.4	17.8	18.0	16.9	17.9	17.5	17.1
November 1982	23.3	21.3	22.6	23.7	21.5	22.1	21.5	21.5
December 1982	24.0	21.4	22.7	24.4	21.5	23.3	22.2	21.5
January 1983	25.2	22.7	24.6	25.7	22.3	25.0	23.5	22.3

Figure 2. Growth (in mm) of hard clams, *Mercenaria mercenaria*, planted at different densities in cages at Cabbage Island, GA. Data points represent the mean of replicate densities. Y = shell length (in mm) and x = time (in months).

Figure 3. Number and species of crabs removed monthly from experimental clam cages located on an intertidal sandflat at Cabbage Island, GA. (The number in parenthesis is the mean carapace width per crab species.)

TABLE 2.

Mean survival percentage per clam density per month for hard clams that were planted in protective cages on an intertidal sandflat at Cabbage Island, GA.

| | Densities | | | | Overall |
Date	509^{-2}	1009 m^{-2}	2018 m^{-2}	3027 m^{-2}	Survival
July 82	89.3	66.2	83.3	59.5	76.5
Aug 82	86.6	95.0	87.6	85.9	87.9
Sep 82	83.0	97.3	94.8	95.5	94.6
Oct 82	100.0	100.0	99.1	99.7	99.6
Nov 82	99.1	99.5	100.0	99.2	99.5
Dec 82	100.0	99.1	100.0	100.0	99.9
Jan 83	98.2	97.7	99.1	99.7	99.1
Final mean survival percentage	62.5	59.0	67.9	48.1	62.4

ranged from 14 to 31% because crabs were not removed monthly but seasonally and they grew large enough to prey upon the clams within the cages (Walker, in preparation).

The following mariculture program is considered feasible for the coastal waters of Georgia. Seed clams (6 mm), which are planted at densities of up to 3,027 m^{-2}, can be grown to a shell length greater than 20 mm within 7 months with greater than 80% survival if they are planted in spring/summer and if crabs are removed from their cages at least monthly. Once the clams reach a shell length of 25 mm, they can be transplanted into plots with baffles or into creeks using shell cover and/or tent structures as protective cover, or left in cages after densities are reduced (Walker, in press).

In Georgia, small feeder creeks (defined as being generally less than 4.5 m in width and several hundred meters in length)

appear to be the best habitat for clam mariculture. Feeder creeks generally drain at low tide or retain standing pools behind oyster reef "dams" which are located at the mouth of or within the creeks. Wild clams may occur in high densities (up to 100 m^{-2}) within feeder creeks. The growth rates of clams in feeder creeks do not differ from those from other habitats; however, clams usually grow faster in sandy substrates (Rhoads and Panella 1970, Kennish and Olsson 1975).

Many clam predators in Georgia do not occur in feeder creeks. The Atlantic oyster drill *Urosalpinx cinerea* (Say) usually occurs at the mouth of and rarely within feeder creeks (Walker 1981). The southern oyster drill *Thais haemastoma* (Conrad) and the starfish *Asterias forbesi* (Desor) have not been found in feeder creeks (Walker 1982). The whelks, *Busycon carica* (Gmelin) and *B. contrarium* (Conrad) generally do not occur in feeder creeks. These creeks also provide a physically less dynamic environment than do major creeks or open areas of the sounds which are exposed to wave action.

Baffles, cages and pens, which were placed in major creeks or open areas of the sounds in Georgia, have not been successful in protecting clams. Cages that were buried in sandy sediment on intertidal flats at Cabbage Island and anchored with approximately 16 kg of bricks were washed out during winter storms, completely buried by shifting sediments, or so severely damaged that clams washed out (Walker, in preparation). Baffles, which were placed in feeder creeks, creeks or areas of the open sound, have met with similar fates. Furthermore, pens, cages and baffles were often vandalized by boaters and sports fishermen or run over by boaters. Beds that are located in small feeder creeks are nominally protected from boats, people (vandals), and wave action, and represent a valuable fishery resource to the state of Georgia.

ACKNOWLEDGMENTS

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WATER QUALITY FLUCTUATIONS IN RESPONSE TO VARIABLE LOADING IN A COMMERCIAL, CLOSED SHEDDING FACILITY FOR BLUE CRABS

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ABSTRACT   A commercial, closed, recirculating seawater facility using biological filters for control of nitrogenous metabolites is described. The volume of each system was 7,560 ℓ. Loading densities of over 1,000 crabs (*Callinectes sapidus* Rathbun) were maintained in each system. Water quality parameters (NH_3-N, NO_2-N, NO_3-N, pH, dissolved oxygen, salinity, temperature, alkalinity) affecting crab survival at molting were monitored for a 2-month period, and safe operational ranges were established. Alkalinity and pH values declined in the systems, demonstrating a limited buffering capacity. Values of NO_3-N exceeding 350 mg/ℓ were observed with no apparent effects to the crabs. Increased molting mortality was observed when concentrations of nitrite approached 1.6 mg/ℓ NO_2-N. Nitrite accumulations were associated with depressed oxygen levels which were induced by peak system loadings or equipment failure. Successful molting rates in excess of 95% were achieved at nitrite and ammonia concentrations below 1 mg/ℓ.

KEY WORDS   Aquaculture, biological filter, blue crab, *Callinectes sapidus*, closed system, molting, water quality

INTRODUCTION

Reported landings for soft-shell crabs have declined drastically in most states harvesting the resource (Jaworski 1971; Otwell et al. 1980; Perry, Ogle and Nicholson 1982). According to Jaworski (1971) the reduced production is attributed to a deterioration of coastal zones and accompanying decline in water quality. Despite the decline in landings, the value of soft-shell crabs has continued to rise in the Gulf of Mexico area and averages $4.50 Kg^{-1} as compared to $1.94 Kg^{-1} in 1970 (Perry et al. 1982).

Traditionally, premolt blue crabs were collected and held in natural waters in floating boxes or pens until they molted (Haefner and Garten 1974). The continuing decline in coastal water quality and subsequent increase in mortality of molting crabs have forced fishermen to turn to onshore facilities to reduce crab losses during molting (Jaworski 1982). The potential value of using closed, recirculating seawater systems for maintaining molting crabs has been demonstrated by a few successful commercial operators (Perry, Ogle and Nicholson 1982). Recirculating systems reduce labor requirements and eliminate the exposure of crabs to deleterious environmental effects during the vulnerable molting period; however, their success has been marginal because of the lack of established design criteria and management guidelines (Van Gorder and Fritch 1980, Ogle et al. 1982).

In the Gulf of Mexico, where crab fishermen are often limited by the availability of premolt blue crabs, shedding operators strive for a molting mortality of less than 5% to maintain production and commercial viability. On the eastern coast of the United States, commercial shedding systems generally have access to an abundance of crabs and, therefore, can absorb a higher crab mortality (5 to 40%).

The operation of a successful, closed, recirculating aquaculture system depends on the maintenance of acceptable water quality. Wheaton (1977) and Spotte (1979) summarized the ability of biological filters in the closed systems to convert ammonia (NH_3), the principal nitrogenous excretory metabolite of Crustacea (Hartenstein 1970), to the relatively nontoxic nitrate (NO_3) by bacterial nitrification.

In 1982, a project was initiated to establish production levels and operating parameters for closed, recirculating seawater systems currently used to hold shedding crabs. This approach provided a unique opportunity to complement experimental research on molting crabs (Manthe et al. in press) with direct observations and data from the commercial sector. In this report we describe the influence of commercial operating procedures on water quality in a large-scale shedding facility.

MATERIALS AND METHODS

Description of Commercial Facility

The commercial shedding operation was located in an uninsulated building in LaCombe, LA. The facility consisted of two separate systems (Figure 1), each with eight holding tanks, two biological filters, one algal tank, and a reservoir. The reservoir was located outside the building and was partially buried in the ground. The facility is a modification of one described by Perry, Ogle and Nicholson
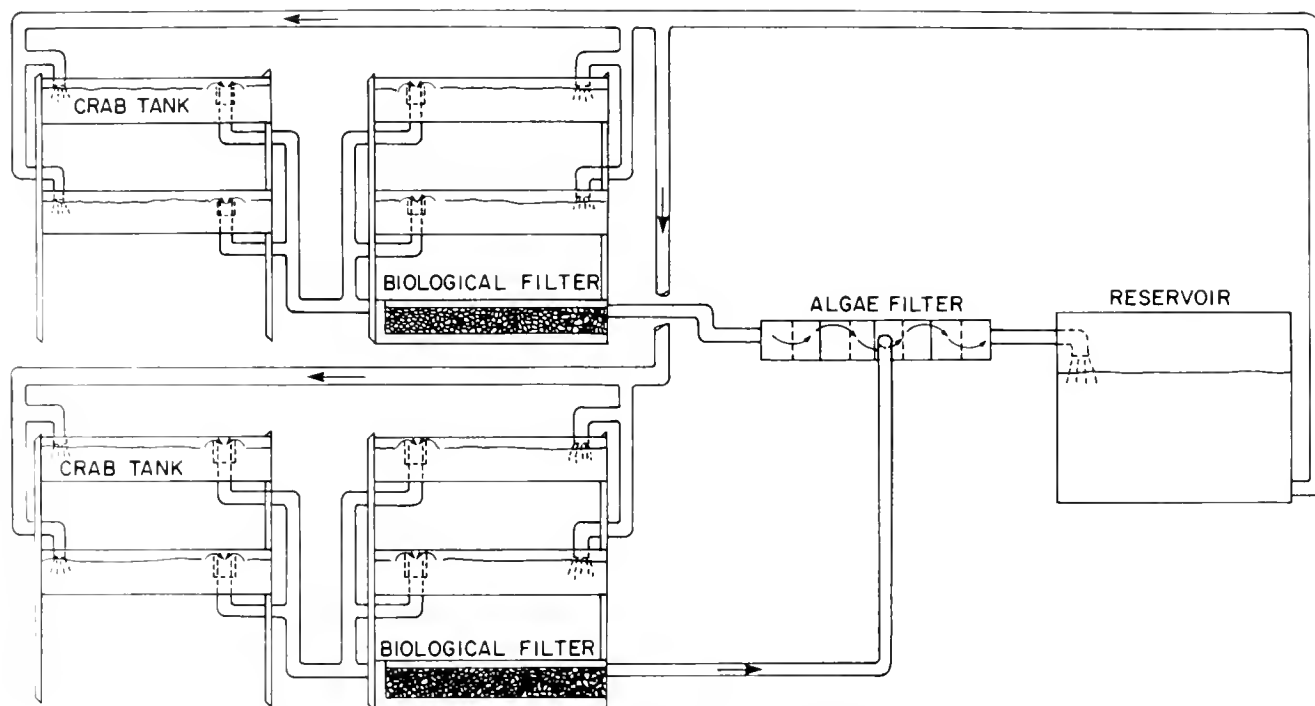
Figure 1. Schematic diagram of one of the commercial systems.

(1982). Descriptions and dimensions of the fiberglass tanks are presented in Table 1.

TABLE 1.

Dimensions of Commercial System.

Description	Length (m)	Width (m)	Depth (m)	Water Depth (m)	Area (m²)	Volume (m³)
Crab tank	2.44	1.07	0.30	0.13	2.61	0.34
Biological Filter	2.44	0.91	0.30	0.24	2.22	0.53
Shell Filter Bed	2.29	0.91	0.08	– –	2.08	0.17
Dolomite Filter Bed	2.29	0.91	0.04	– –	2.08	0.08
Carbon Filter Bed	2.29	0.91	0.03	– –	2.08	0.06
Algal Filter	2.44	0.91	0.30	0.24	2.22	0.53
Holding Reservoir	2.74	1.37	1.52	1.07	3.75	4.02

Water levels in the crab tanks were controlled by 12.7-cm standpipes constructed from 3.2-cm polyvinylchloride (PVC) pipe. Water input to the discharge nozzle in the crab tanks consisted of capped 1.3-cm PVC pipe with two 0.3 cm holes to promote active aeration in the tanks.

The biological filters were constructed with a fiberglass partition that was positioned 15.2 cm from one end of the tank with holes drilled in the lower 2.5 cm of the partition. The head chamber received the overflow from the crab tanks

through the standpipe that discharged beneath the water level in the head chamber. The function of the head chamber was to direct water flow under the submerged, updraft, biological filter. The biological filter consisted of a 7.6-cm layer of washed clam shells (*Rangia cuneata*) (2- to 3-cm diameter) on the bottom, overlaid by 3.8 cm of dolomite (3-mm grain size), and 2.5 cm of activated carbon (1- to 3-mm grain size) (Figure 2). Each layer of medium was separated by nylon window screen. The filter bed rested on 1.3-cm egg crate louvering supported by 2.5-cm PVC pipe lengths. The water level in the biological filter was approximately 5 cm above the top of the activated carbon bed; overflow to the algal tank was provided through a 5.1-cm PVC pipe. Theoretically, the biological filters performed two main functions: mineralization and nitrification. These functions take toxic nitrogen waste products produced by the crabs and convert them to relatively nontoxic forms. By design rational, buffering was accomplished using carbonate filtrants (shell and dolomite). and physical adsorption of dissolved organic carbon occurred on activated marine carbon.

The algal tank contained 11 baffles that alternately extended to within 7.6 cm of the tank sides. Attached algae grew on the sides of the baffles and water flowed in a serpentine fashion from one end of the tank to the other. Another 5.1-cm PVC pipe, from the other four crab tanks and biological filter in each system, drained into the algal tank half way through each filter. Each algal filter was illuminated by two 1.2-m fluorescent fixtures which contained four 40-W Grow Lux® lights. Plants in the
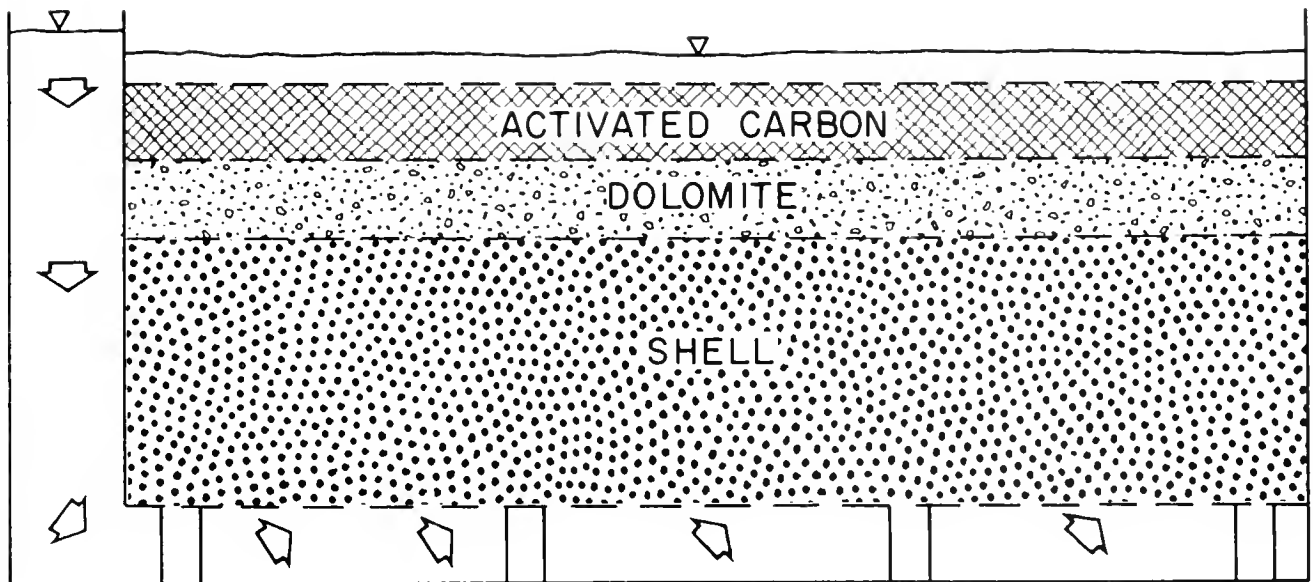
Figure 2. Cross section of biological filter.

systems included water milfoil (*Myriophyllum* sp.) that floated on the algal filter surface, and attached filamentous green algae on the filter walls. No algae were harvested from either of the systems and the algal filters were provided with a constant light regime. Water flowed by gravity from the algal filters and was carried by 7.6-cm PVC pipe through the wall of the building to the partially buried reservoir outside. The algal filters were incorporated into the system to remove nitrate, the end product of nitrification.

The large reservoir helped to buffer any rapid changes in water quality in the systems. Rapid water quality changes (typically transitional increases in ammonia and nitrite) can be associated with the introduction of a large number of crabs to a system that has been acclimated to a smaller number of crabs, a common practice in commercial operations. Water was constantly circulated from the reservoir via a 5.1-cm PVC pipe to a 0.25 kW pump (model Dayton® 6K695). The pipe was screened to prevent the intake of large debris. The water was then distributed through a 3.2-cm overhead PVC pipe to the crab tanks by a series of 1.9-cm PVC valves and tees. Water was sprayed under pressure into the crab tanks at a constant (total system) flow rate of 83.3 ℓ/min.

Methods

Artificial seawater (Rila Mix®) was used in the commercial facility. The two systems were constructed and operated one year prior to the study and had been shut down in the winter of 1982–83. Start up in March of 1983 consisted of turning on the pumps and diluting the systems to volume with fresh well water. Fresh water was added to the systems to offset evaporation, but no water changes were made during the period of observation. Intermolt blue crabs and miscellaneous estuarine fish were used to acclimate the

biological filters until April. During the study, premolt blue crabs ranging from 10 to 15 cm in carapace width were taken from Lake Pontchartrain, LA, and held in the systems. Vinyl-coated, wire-mesh enclosures 0.3 cm in diameter isolated crabs that had molted. System management included visual inspections every 3 to 4 hours to collect soft-shell crabs and to remove mortalities, debris, and exuviae. Crabs in the shedding systems were not fed at any time. Mean residence time for a typical crab in the system was estimated to be 7 days.

Systems were monitored at 9:00 a.m. each day for temperature, salinity, dissolved oxygen, ammonia, nitrite, and pH. A 1 ℓ sample of water was taken from each system and analyzed immediately for total ammonia and nitrite. Determinations of alkalinity levels and nitrate concentrations were made on a weekly basis. Techniques and instrumentation to measure the above-mentioned parameters are listed in Table 2. Crab densities in each system were recorded daily after crab additions were made in the afternoon (2:00 p.m.). Data were collected through the spring shedding season of 1983, and systems were numbered (1 and 2, respectively) for reporting and identification during the interpretation of results.

RESULTS AND DISCUSSION

pH, Alkalinity, Salinity, Nitrate

Water quality observations for pH, alkalinity, and nitrate are illustrated in Figure 3. Both systems behaved similarly with regard to the monitored parameters. Each system initially exhibited a pH of 7.7, and declined to values between 7.0 and 7.2. This reduction of pH was associated with a decline in alkalinity. The systems displayed initial alkalinities of 70 mg/ℓ $CaCO_3$, declining to values as low as

TABLE 2.

Measurements Taken and Techniques.

Parameter	Instrument or Test	Reference
Total ammonia as NH_3-N	Orion 95-10 ammonia electrode/ Orion 701A digital ionalyzer	APHA (1980)
Nitrite as NO_2-N	Bausch and Lomb Spectronic 20, Spectrophotometer	Sulfanilamide-based colori- metric reaction APHA (1980)
Oxygen as O_2	Yellow Springs Instrument Co. Dissolved oxygen meter, Model 51	
Salinity	American Optical Refractometer	
pH	Mini (Model 47) pH meter	
Nitrate as NO_3-N	Modified hydrazine reduction	Spotte (1979)
Alkalinity as $CaCO_3$	Titration	APHA (1980)

30 mg/ℓ $CaCO_3$, suggesting a limited capability of the dolomite and shell layers to buffer pH changes. These findings are consistent with the observations of Bower et al. (1981), who noted the limited ability of calcareous filtrants to maintain pH above 8.0. In this study, pH values fell within the 7.0 to 8.5 range of optimum nitrification rates for biological filters (Wheaton 1977), although filters can be acclimated to pH values lower than 7.0 (Haug and McCarty 1972). We conclude that the dolomite/shell bed was sufficient for control of pH above 7.0 even after two years of operation with no filter maintenance, and that this pH apparently does not adversely affect the crabs. In fact, the lower pH may be beneficial in that it reduces ammonia toxicity because of the equilibrium reaction between NH_4^+ and NH_3 (Wheaton 1977, Spotte 1979).

The concentration of nitrates increased throughout the study and was directly related to the increased crab loadings of both systems. Nitrate levels in systems 1 and 2 were 171 and 214 mg/ℓ NO_3-N, respectively, at the beginning of the observation period. Differences in these accumulated nitrate concentrations apparently resulted from unequal numbers of crabs in each system and the total time that the individual systems were operated in the year prior to the study (system 2 was operated for a longer period in 1982). Observations of the algal filters revealed little or no algal growth despite efforts to reintroduce algae from local sources and another commercial system. Values exceeding 350 mg/ℓ NO_3-N were observed at the end of this study with no apparent deleterious effects. Nitrate is generally not toxic to marine organisms even at elevated levels (Hirayama 1974, Siddall 1974). Salinity in the systems remained constant at 4 and 5 ppt in systems 1 and 2, respectively.

Ammonia, Nitrite, Temperature, Dissolved Oxygen

Ammonia and nitrite increases were closely related to

increases in crab concentrations (Figure 4), and both systems showed comparable results in terms of water quality and crab loadings. In system 1, total ammonia concentrations remained under 0.4 mg/ℓ NH_3-N regardless of crab density. Nitrite concentrations, however, increased to 1.6 mg/ℓ NO_2-N during a period of heavy loading. During the heaviest crab loading in system 2, ammonia levels approached 1.0 mg/ℓ NH_3-N, with a similar increase in nitrite. On May 5, increased mortality of molting crabs was observed in system 1 when nitrite concentrations approached 1.6 mg/ℓ NO_2-N. A pump malfunction occurred in system 2 on May 28, and nitrite concentrations subsequently increased. Concentrations above 1.2 mg/ℓ NO_2-N were observed on May 29, but returned to low levels the following day. Mevel and Chamroux (1981) found that during similar pump malfunctions nitrate levels decreased and nitrite levels increased. They concluded that nitrate was reduced to nitrite when oxygenation of the environment was deficient, and that bacteria were responsible for the dissimilatory nitrate reduction. This might explain the increase of nitrite observed in our study during the pump malfunction.

Figure 5 illustrates the temperature and dissolved oxygen levels recorded in the systems under study. Water temperature in the systems equilibrated rapidly to ambient air temperatures which varied from $11°$ to $27°C$. Higher temperatures decreased the overall carrying capacity of the systems. This was supported by the inverse effect of temperature on the saturation levels of dissolved oxygen (Figure 5). Higher temperatures also increased the metabolic rates of both the heterotrophic and nitrifying bacteria (Wild et al. 1971) and the crabs (Laird and Haefner 1976). Oxygen levels in both systems were influenced by this increased biological activity. Oxygen measurements in the commercial systems were taken between the biological filter and the algal tank. Because of the large surface area on the top of the upflow biological filters, some surface reaeration may have occurred upstream of the dissolved oxygen measurement point; however, in both commercial systems the lowest dissolved oxygen values were concurrent with peak values of nitrite and crab loadings, thereby suggesting intense activity in the biological filter. These observations were consistent with those of Manthe et al. (in press) which identified dissolved oxygen as the factor limiting the efficiency of nitrification beds in experimental crab shedding systems of the same design. That study also demonstrated that as dissolved oxygen concentration decreased, toxic nitrite concentrations increased and significant crab mortality occurred.

In the latter part of this study, the biological filters began to overflow in the head chambers. Accumulations of detritus were observed in the nylon screens separating the different layers of medium in the filter bed. These accumulations may have led to the short circuiting of the filter bed and thus reduced its nitrification ability. Annual breakdown
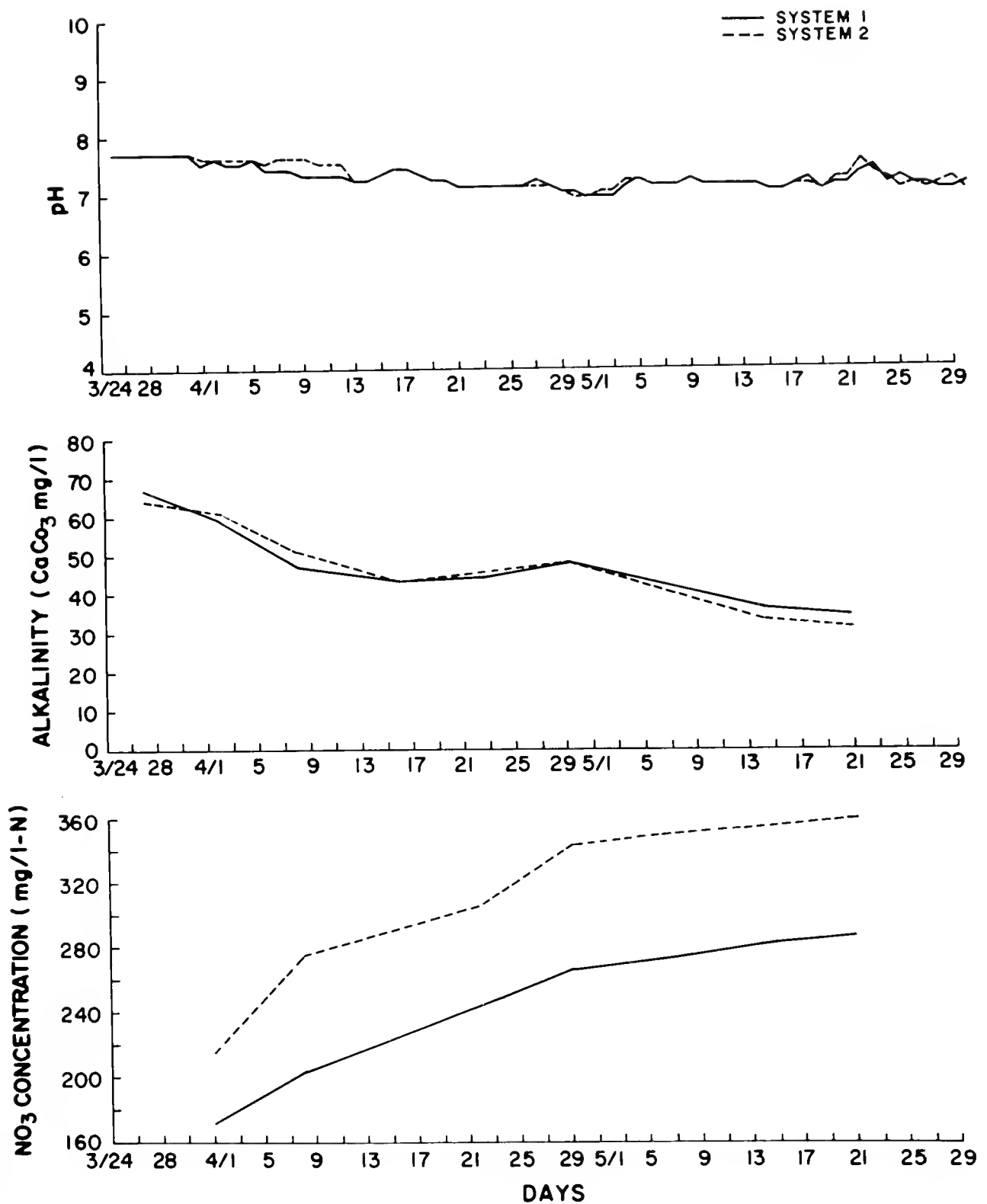
Figure 3. Supporting water quality parameters for the commercial systems (pH, alkalinity, and nitrate).
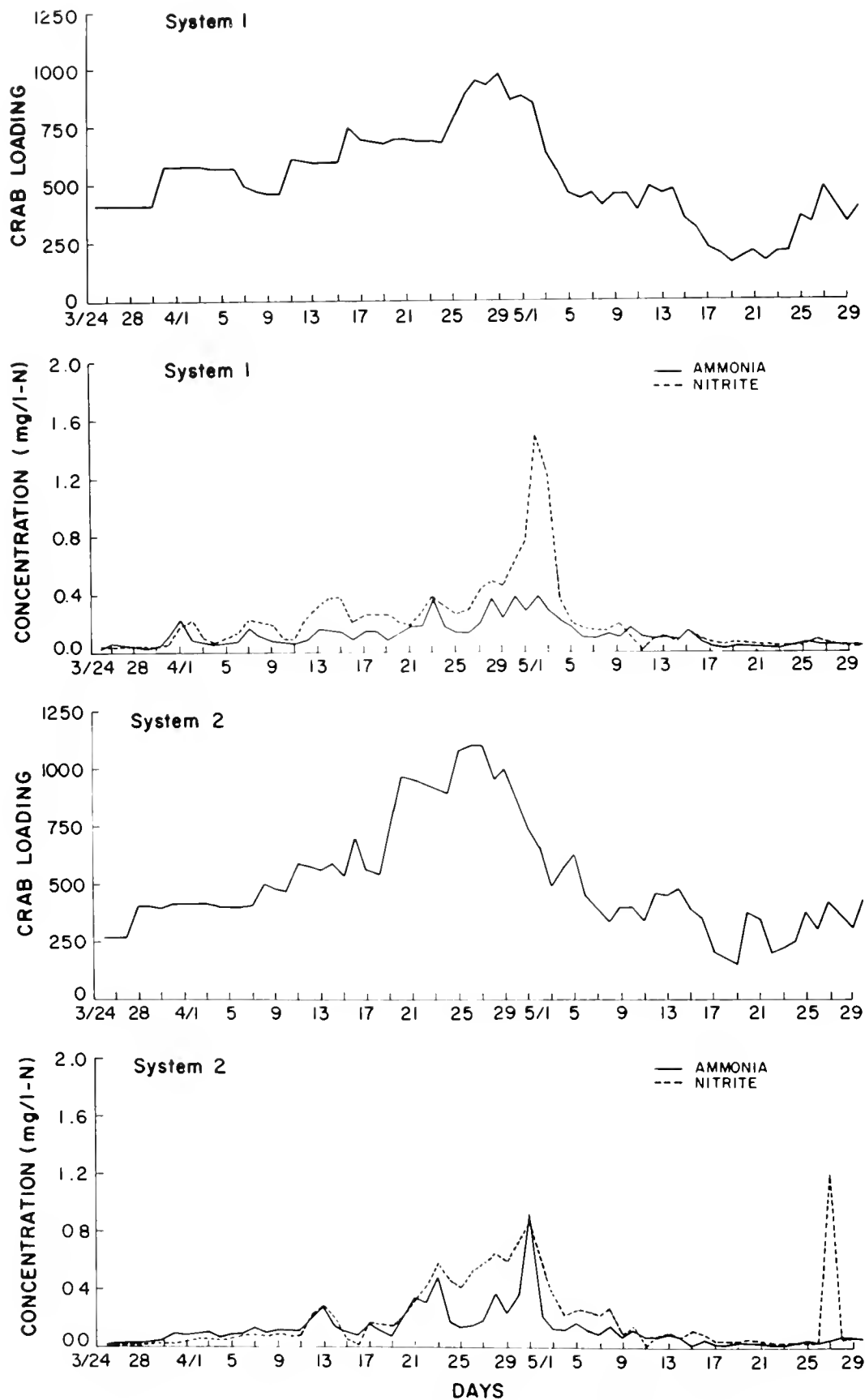
Figure 4. Ammonia and nitrite concentrations in relation to crab densities (systems 1 and 2).
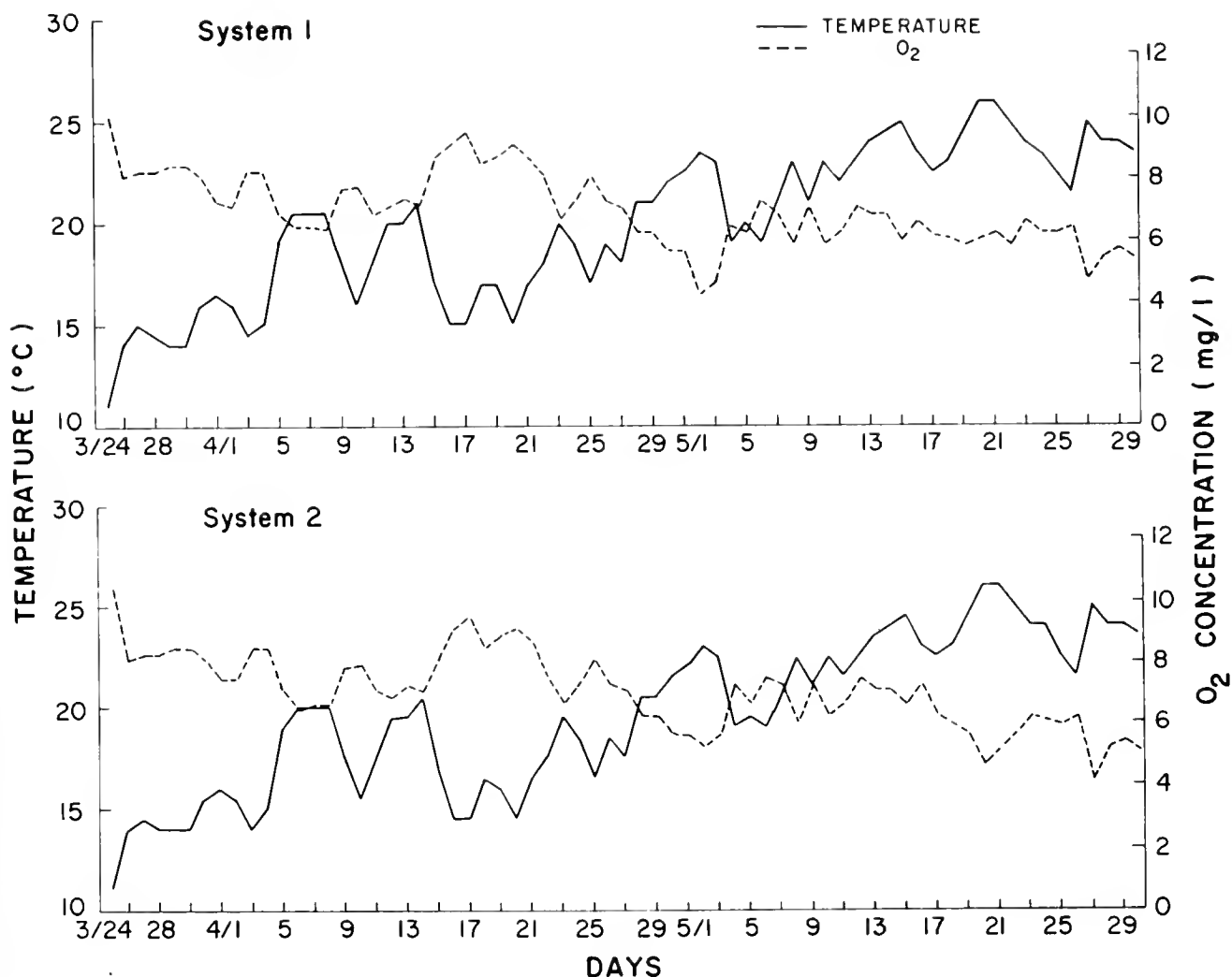
Figure 5. Temperature and dissolved oxygen values (systems 1 and 2).

and cleaning of the biological filter should be considered when using this design.

Throughout the study, acceptable water quality was maintained with this filter design and successful molting rates of more than 95% were observed in the facility. Loading values of over 1,000 crabs were maintained by each system over the observed period. Table 3 summarizes observed operational ranges for selected water quality parameters in the systems studied.

TABLE 3.

Observed operational ranges for selected water quality parameters.

Parameter	Range
Total ammonia	$0 - 1 \text{ mg} \cdot \ell^{-1}$
Nitrite	$0 - 1 \text{ mg} \cdot \ell^{-1}$
Nitrate	$0 - 350 \text{ mg} \cdot \ell^{-1}$
pH	$7 - 8$
Temperature	$11^\circ - 27^\circ C$

Decreased molting success was observed when concentrations of nitrite approached $1.6 \text{ mg} \cdot \ell^{-1}$ NO_2-N. Total ammonia levels did not rise above $1.0 \text{ mg} \cdot \ell^{-1}$ NH_3-N and these levels had no apparent harmful impact on the molting crabs. In both systems the lowest dissolved oxygen values were concurrent with peak values of crab density and nitrite, indicating an intense oxygen demand in the biological filters to process the increased production of nitrogenous waste. Monitoring of nitrite and dissolved oxygen concentrations appear to be of critical importance to commercial softshell production in closed systems.

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BLUE CRAB (*CALLINECTES SAPIDUS* RATHBUN) POPULATIONS IN MID–CHESAPEAKE BAY IN THE VICINITY OF THE CALVERT CLIFFS NUCLEAR POWER PLANT, 1968–1981

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ABSTRACT Population data of the blue crab *Callinectes sapidus* Rathbun were collected from 1968 to 1981 to determine the affects of waste heat from the Calvert Cliffs Nuclear Power Plant on abundance, size distribution, sex ratio, and seasonality of occurrence. Crabs were sampled using commercial crab pots of 25-mm-mesh set within (Plant Site) and outside (Kenwood Beach and Rocky Point) the main area of thermal influence. Five pots per station were fished four days per week during alternate weeks from May to November or December. Crabs were sexed, measured, and weighed by sex. In 14 years, a total of 10,600 pot samples yielded 57,078 crabs (5.38 per pot) of which 74.1% were legal size ($\geq$ 127 mm carapace width) and 51.5% were males. During seven pre-operational years (1968–74), the number of crabs per pot averaged 4.15 at Kenwood Beach (32.6%), 4.12 at Plant Site (32.4%), and 4.46 at Rocky Point (35.0%). During seven operational years (1975–81), the number of crabs per pot averaged 6.24 at Kenwood Beach (33.3%), 6.37 at Plant Site (34.0%), and 6.15 at Rocky Point (32.8%). Increased catch during the operational period was due to extreme abundance in 1981 when the mean catch was nearly 17 crabs per pot. Ten population variables were tested for differences between pre-operational and operational periods and among stations and years. Data analyses revealed many differences among years due to natural fluctuations in the size and structure of Chesapeake Bay blue crab populations. Two station differences were detected; males at Kenwood Beach were slightly larger than at the other stations (p < 0.01), and percent males at Kenwood Beach was higher than at Rocky Point (p < 0.01). The overall similarity of stations and periods indicates no evidence of any detrimental effect on the crab populations caused by operation of the Calvert Cliffs Nuclear Power Plant.

KEY WORDS: blue crab, *Callinectes sapidus*, Calvert Cliffs, Chesapeake Bay, nuclear power plant, thermal effluent

INTRODUCTION

For nearly a century the blue crab *Callinectes sapidus* Rathbun has been the basis of one of the major commercial fisheries in the Chesapeake Bay area. From the late 1940's to the late 1950's the annual catch averaged nearly 27.2×10^6 kg (60×10^6 lb) valued at $3 million (Van Engel 1958). From 1968 to 1975 annual landings increased to almost 29.9×10^6 kg (66×10^6 lb) valued at $7.7 million (U.S. Fish and Wildlife Service 1970a, b; National Marine Fisheries Service 1972–1976a, b). From 1976 to 1980 mean landings fell to 26.3×10^6 kg (58×10^6 lb), but dockside value increased to $13 million (National Marine Fisheries Service 1977–1979a, b, 1980, 1981, 1982). Record landings occurred in 1981 with 46.3×10^6 kg (102×10^6 lb) valued at $27 million (National Marine Fisheries Service 1982).

The size and economic importance of this fishery are obvious cause for concern regarding industrial construction which could affect it. Mihursky and Kennedy (1967) discussed problems associated with heated discharges from power plants including the fact that many plants discharge water heated to 38–46°C. Tagatz (1969) also indicated that power plant discharges of heated waste water might be a threat to blue crabs.

In 1968 Baltimore Gas and Electric Company began construction of the Calvert Cliffs Nuclear Power Plant (CCNPP), a two-unit generating station located on Chesapeake Bay in Calvert County, Maryland, about 15 km north of the mouth of Patuxent River. Bay water is used in a once-through cooling system at a rate of 9.08×10^6 ℓ/min, heated 6.7°C (maximum) above ambient and discharged at 2.7 m/sec through a high-velocity jet 260 m from shore (Baltimore Gas and Electric Company 1970). Mixing of the

discharge and receiving water is rapid and the area enclosed by the +2°C isotherm is only 0.34 km² assuming 10% recirculation (Academy of Natural Sciences of Philadelphia et al. 1980); however, thermal increases of 0.5 to 1.0°C above ambient have been detected more than 3 km away.

In addition to being one of the most abundant commercial species in the Chesapeake Bay, the blue crab is also one of the most tolerant of a wide range of salinities and temperatures. Tagatz (1969) has shown that at salinities of 7 ppt, somewhat lower than the 10 to 15 ppt at Calvert Cliffs, 50% of the crabs acclimated to 22°C will survive 48 hours at a temperature of 36.9°C. Burton (1978) exposed juvenile blue crabs acclimated at 15 and 25°C to a rapid 10°C increase, held them at the elevated temperature for four minutes, and returned them to the acclimation temperature over a 15-minute decay period. Weight-specific oxygen consumption indicated that responses were due to normal physiological temperature compensation and not to thermal stress. He concluded that increases of up to 10°C would have minimal adverse seasonal effect on blue crabs when exposure time was held to 20 minutes. Because maximum temperatures near the CCNPP discharge are several degrees below 37°C and because blue crabs are strong swimmers capable of relatively rapid movement, mortalities resulting from the thermal discharge were not expected. Sublethal temperatures, however, could affect the distribution or structure of the total population, so that numbers of crabs, their mean sizes or sex ratios would be abnormally altered. Because large fluctuations in annual abundance of blue crabs have been well documented

(Pearson 1948, Van Engel 1958, Tagatz 1965), this study was designed to examine abundance, seasonality of occurrence, sex ratio, and size-frequency distribution of the crab populations in the vicinity of the CCNPP over several years, and to ascertain whether any significant changes in these parameters have resulted from plant operation. The plant became operational in early 1975 and Unit 1 began commercial production in May 1975; Unit 2 began operation in 1977. Thus seven years of pre-operational data and seven years of operational data were collected from 1968 to 1981. This paper reports the effects of power plant operation on the local crab populations and provides descriptive statistics of these populations over a 14-year period.

MATERIALS AND METHODS

Stations

The center of the study area was adjacent to the Calvert Cliffs plant site located approximately 7.6 km northwest of Cove Point on the western shore of Chesapeake Bay (Figure 1). Although this station was within 100 m of the discharge, it did not receive the full impact of the thermal plume. Temperatures averaged $1°$ to $2°C$ above ambient during operational years; water depth was approximately 2.5 m. The upper station was located near Kenwood Beach, 6.4 km from the discharge at 3.7 to 4.6 m water depth; the lower station was southeast of Rocky Point 3.8 km from the discharge at 3.5 m water depth. The Kenwood Beach and Rocky Point stations were outside of the predicted area of thermal affect when they were established in 1968. Plant operation, however, did result in occasional temperature increases of up to $1°C$ at Rocky Point; Kenwood Beach remained unaffected. Salinity at the Rocky Point station averaged 1 to 2 ppt higher than at Kenwood Beach.
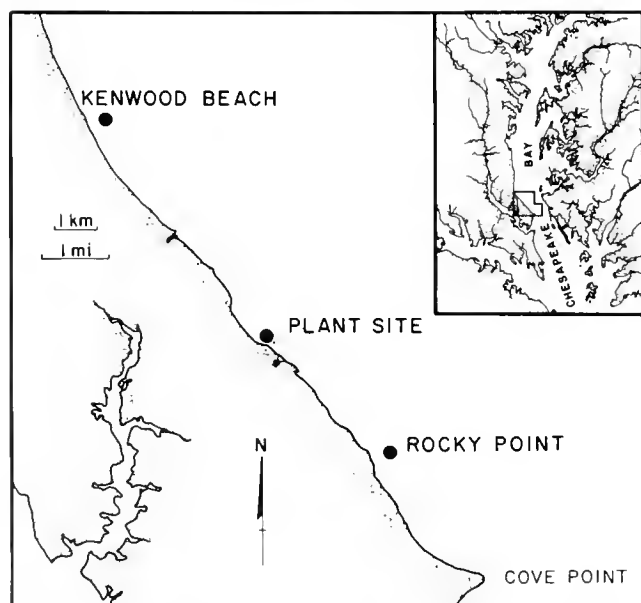

Figure 1. Locations of crab pots in mid-Chesapeake Bay from 1968 to 1981.

Study Design

Commercial potting techniques (Van Engel 1962) and crab pots of 25-mm-mesh were used to sample the crab populations at the three stations from spring (generally early May) until late fall when water temperatures declined to levels at which crabs became inactive ($10-12°C$ in November or December). Commercial crab pots are generally constructed of 38-mm-mesh and will hold few crabs less than 76 mm (3 in.) in carapace width; however, the smaller mesh pots used in this study allowed some crabs less than 51 mm (2 in.) to be caught.

During alternate weeks throughout the season, five pots (three in 1968) at each station were baited daily with menhaden and fished for four successive days. Station catches were weighed by sex and all crabs were measured to the nearest one-eighth-inch (3 mm). Field measurements were later converted to metric.

Bottom temperature and salinity were determined monthly by thermistor probe and titration, respectively, from 1968 to 1978 and daily during the weeks fished from 1979 to 1981 with a Beckman RS5-3 portable salinometer. Dissolved-oxygen concentrations were determined monthly through 1974 and daily thereafter either by Winkler titration or with a YSI Model 57 dissolved-oxygen meter.

Statistical Analysis

A cross-nested analysis of variance (Hicks 1973) was used to compare various parameters of the crab populations and thus test for differences between the pre-operational and operational periods. Population parameters included the number caught per pot for legal size crabs and for total crabs, mean widths and weights of males, females, and combined sexes, the percent legal size crabs, and percent males. The crossed effects in this analysis were station and year and the nested effect was year within period. The period effect was tested against the year (period) error term while other effects were tested against the highest order interaction term for this model. All parameters except percent legal size and percent male were yearly averages; because averages of large samples tend to be normally distributed, no transformation was required. The percent legal size and percent males at each station for each year were transformed by arcsine-squareroot transformation to stabilize variances and improve normality (Thöni 1967).

Percent males were also examined over the entire 14-year period by analysis of covariance (Hicks 1973) using logit-transformed data (Cox 1970).

RESULTS AND DISCUSSION

Summaries of the annual blue crab catches made in the Calvert Cliffs area during 1968–1974 (pre-operational) and during 1975–81 (operational) are presented in Tables 1 and 2, respectively. In 14 years of study, 10,600 pot samples produced 57,078 crabs (5.38 per pot) of which 51.5% were males and 74.1% were legal size (≥ 127 mm carapace width).

TABLE 1.

Summary of abundance, size, and sex composition of blue crab catches near the Calvert Cliffs
Nuclear Power Plant from 1968 to 1974 (pre-operational period).

	1968	1969	1970	1971	1972	1973	1974	Grand Mean
Total number	239	2,833	1,493	4,792	3,041	3,059	3,970	2,775
Number of males	158	1,995	914	2,657	1,794	1,753	2,366	1,662
Number of females	81	838	579	2,135	1,247	1,306	1,604	1,113
Percent males	66.1	70.4	61.2	55.4	59.0	57.3	59.6	61.3*
Total weight (kg)	48	367	228	709	448	479	630	416
Mean weight per crab (g)	201	130	153	148	147	157	159	155*
Male weight (kg)	33	262	145	417	277	295	400	261
Mean weight per male (g)	209	131	159	157	154	168	169	164*
Female weight (kg)	15	106	83	293	171	185	230	155
Mean weight per female (g)	185	126	143	137	137	142	143	145*
Number of legal size crabs ($\geq$ 127 mm)	206	2,006	1,128	3,629	2,195	2,388	2,942	2,071
Number of sublegal size crabs	33	827	365	1,163	846	671	1,028	705
Percent legal	86.2	70.8	76.5	75.7	72.2	78.1	74.1	76.2*
Mean crab width (mm)	153	134	140	138	137	143	141	141*
Mean width of males (mm)	151	134	139	135	134	141	139	139*
Mean width of females (mm)	157	134	142	141	141	146	144	144*
Total pots fished	281	472	564	760	795	898	809	654
Number of crabs per pot	0.85	6.00	2.65	6.31	3.83	3.41	4.91	3.99*
Number of legal size crabs per pot	0.73	4.25	2.00	4.78	2.76	2.66	3.64	2.97*

*Grand means of means and percents are unweighted.

TABLE 2.

Summary of abundance, size, and sex composition of blue crab catches near the Calvert Cliffs
Nuclear Power Plant from 1975 to 1981 (operational period).

	1975	1976	1977	1978	1979	1980	1981	Grand Mean
Total number	4,902	2,845	2,089	3,476	5,740	3,493	15,106	5,379
Number of males	2,381	1,245	1,080	1,707	3,034	1,464	6,853	2,538
Number of females	2,521	1,600	1,009	1,769	2,706	2,029	8,253	2,841
Percent males	48.6	43.8	51.7	49.1	52.8	41.9	45.4	47.6*
Total weight (kg)	748	392	383	552	864	638	1,972	793
Mean weight per crab (g)	153	138	183	159	151	183	131	157*
Male weight (kg)	384	172	217	285	478	281	863	383
Mean weight per male (g)	161	138	201	167	158	192	126	163*
Female weight (kg)	364	220	165	267	386	357	1,110	410
Mean weight per female (g)	144	138	164	151	143	176	134	150*
Number of legal size crabs ($\geq$ 127 mm)	4,006	1,922	1,737	2,598	4,449	2,877	10,211	3,971
Number of sublegal size crabs	896	923	352	878	1,291	616	4,895	1,407
Percent legal	81.7	67.6	83.1	74.7	77.5	82.4	67.6	76.4*
Mean crab width (mm)	144	137	149	143	142	149	135	143*
Mean width of males (mm)	140	131	148	138	138	143	126	138*
Mean width of females (mm)	148	143	151	148	146	153	142	147*
Total pots fished	902	841	756	886	879	861	896	860
Number of crabs per pot	5.43	3.38	2.76	3.92	6.53	4.06	16.86	6.13*
Number of legal size crabs per pot	4.44	2.29	2.30	2.93	5.06	3.34	11.40	4.54*

*Grand means of means and percents are unweighted.

Considerable variation in annual population size, individual mean size, and sex ratio is evident in data from Tables 1 and 2 with significant differences among years for all variables examined by analysis of variance (ANOVA) (all p < 0.01). There were, however, many similarities between the two periods. For example, the annual mean number of crabs caught per pot during the pre-operational period ranged from 0.85 to 6.31 (a 7.4:1 ratio) and during the operational period ranged from 2.76 to 16.86 (a 6.1:1 ratio). Mean crab weights were similar during the two periods (155 and 157 g, respectively), as were the percentages of legal-size crabs caught (76.2% and 76.4%, respectively). Mean carapace widths were also nearly the same at 141 mm and 143 mm, respectively. Thus it appears that year-to-year fluctuations were due to natural changes in population structure and not to operation of the CCNPP.

Statistical differences among stations were detected for only two of the ten variables tested. Male crabs were significantly larger (p < 0.01) at Kenwood Beach (138.6 mm carapace width) than at the Plant Site (135.6 mm) or at Rocky Point (136.3 mm). Although these sizes differ statistically, there is little biological significance to the differences.

Percent males were also greater at Kenwood Beach (55%) than at Rocky Point (48%) (p < 0.01); the 51% males at Plant Site differed from neither. This difference probably resulted from the higher salinities at Rocky Point than at Kenwood Beach because the ratio of males to females normally decreases as salinity increases (Lippson 1973).

Commercial landings in Maryland during 1968–1981 ranged from about 4.5 to nearly 27.2×10^6 kg (10 to 60 $\times$ 10^6 lb), while the numbers of crabs caught per pot in the study area ranged from less than 1 to nearly 17 (Figure 2). Linear regression analysis revealed a high correlation (r^2 = 0.88) between these two data sets indicating that crab abundances near Calvert Cliffs were representative of commercial catches in the Maryland portion of Chesapeake Bay. The number of legal-size crabs caught per pot ranged from 0.73 to 11.40 (Tables 1 and 2) and also correlated well with Maryland landings (r^2 = 0.87).

Percents of annual legal-size crabs caught were much more stable than abundances, ranging from 68% in 1976 and 1981 to 86% in 1968 (Tables 1 and 2). During a given year, however, the percent of legal-size crabs caught varied considerably. Figure 3 shows the percentage of legal-size crabs caught by station for the weeks fished during 1981 and illustrates this seasonal variation. In May 1981 the population consisted of crabs hatched in 1979 and 1980. About 60% were 1979 crabs which were already of legal size; the remainder were sublegal size from the 1980 spring hatch. As the 1979 crabs were removed from the population and more small 1980 crabs were recruited to the area, the percent of legal-size crabs decreased to below 20% in June. As the 1980 crabs grew during the season, the percent of legal-size crabs gradually increased until a peak above

90% was reached in the fall. During November the percent of legal-size crabs decreased again, possibly from the off-shore movement of large crabs and from the recruitment of small crabs hatched in early 1981 which were becoming large enough (65 mm; Van Engel 1958) to be caught in pots. The high correlation between the annual percent of legal size and mean crab weight (r^2 = 0.78) is shown in Figure 4. The lowest annual mean weights were 130 g and 131 g in 1969 and 1981, respectively, both following years of high reproductive success. The large proportion of light-weight, sublegal-size crabs resulted in low mean weights and low legal-size percentages (70.8 and 67.6%). In contrast, 1968 followed a year of poor recruitment and juveniles were scare; the mean weight was 201 g and the percent of legal size was above 86%.
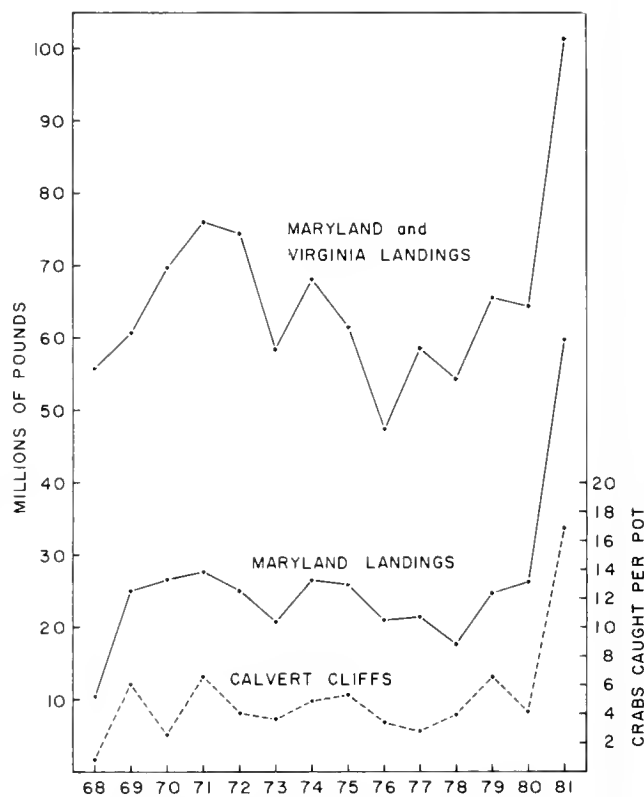
Figure 2. Commercial blue crab landings and catch per pot in the Calvert Cliffs study area from 1968 to 1981.

During the 14-year study period, females averaging 145 mm in carapace width were 7 mm larger than males (138 mm). The mean weight of the males (164 g), however, was 17 g more than females (147 g). This is consistent with other studies of Chesapeake Bay (Newcombe et al. 1949), Florida (Tagatz 1965), and Texas (Pullen and Trent 1970), which showed that males of a given width are heavier than females of the same width. Annual mean widths ranged from 134 to 153 mm (Tables 1 and 2), much smaller than the 155-, 158- and 166-mm means for crabs caught by pots in three areas of the St. Johns River, Florida (Tagatz 1965).
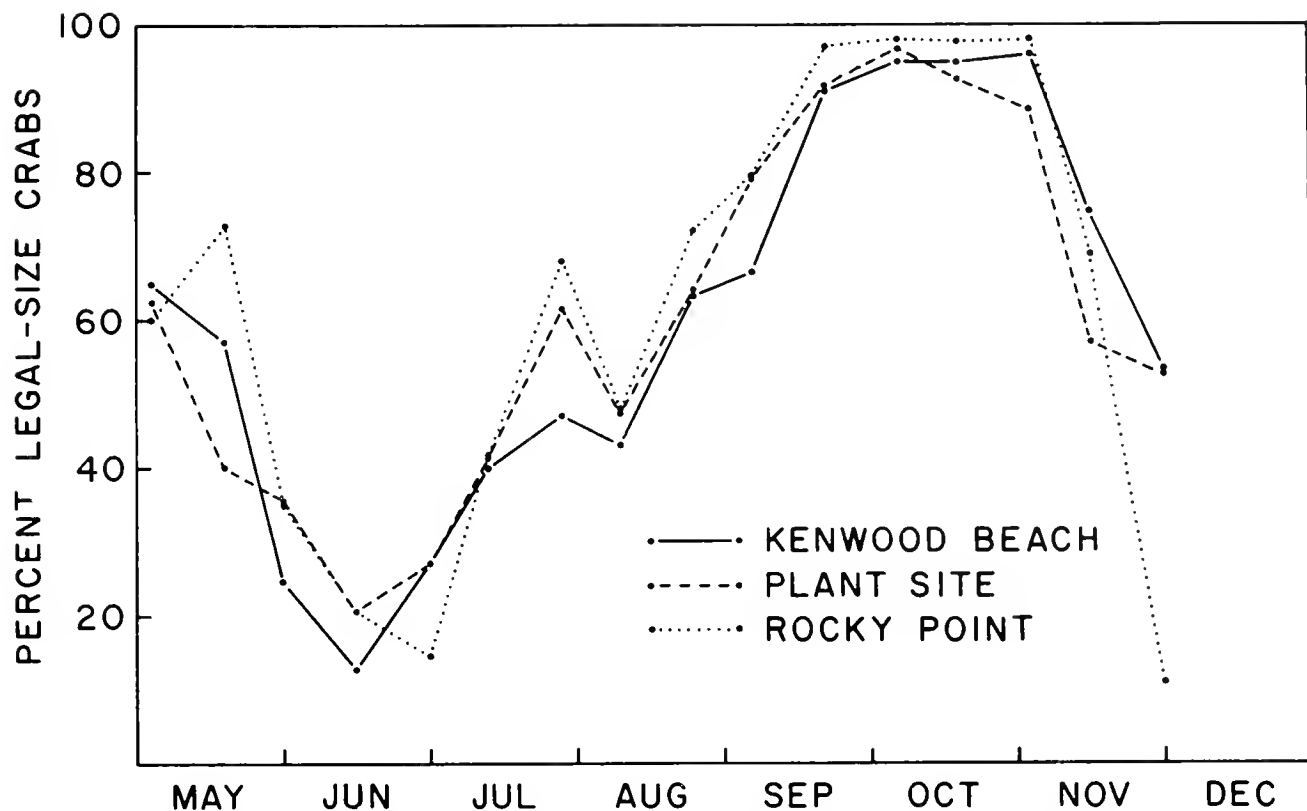
Figure 3. Percent of catch consisting of legal-size crabs ($\geq$ 127 mm carapace width) at three stations during 1981.

Figure 4. Linear regression of annual percent of legal-size crabs caught and mean crab weight.

Crabs in southern states apparently grow to larger sizes than those in Chesapeake Bay. The largest crab used by Newcombe et al. (1949) in their formulation of width-weight curves for Chesapeake Bay crabs was 201 mm and the largest crab from the present study was 213 mm. Of the 57,078 crabs caught near Calvert Cliffs, only 6 exceeded 203 mm (8 in.). In contrast, Tagatz (1965) reported a 246-mm crab from Florida and 240-mm crabs are known from Texas.

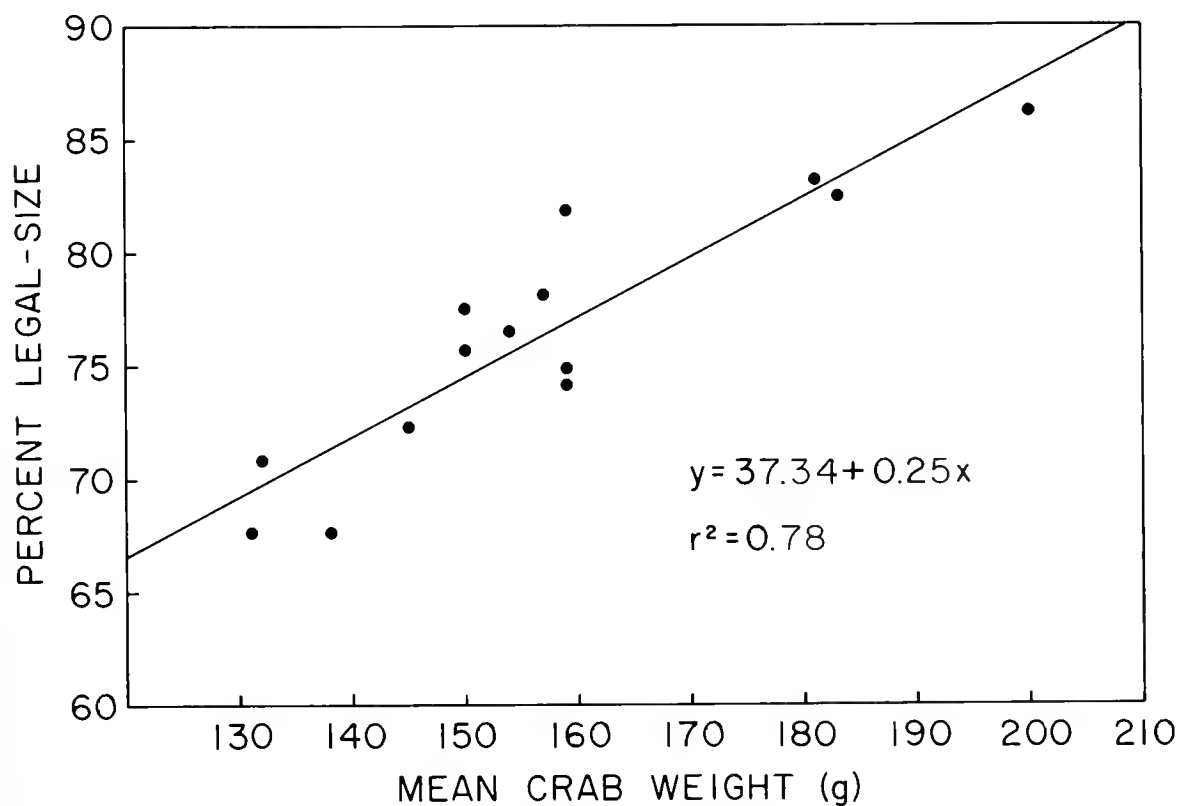Table 3 lists numbers of males and females, their weights, and the mean number caught per pot at each station. Although station differences were apparent within years, trends were similar as were overall means. Except for 1968 and 1981, the poorest and best years of the study, respectively, the catch ranged from about two to seven crabs per pot. For the 14-year study period, Kenwood Beach pots produced a mean of 5.32 crabs per pot (32.9% of the total), while Plant Site pots produced 5.40 crabs per pot (33.4%), and Rocky Point produced 5.43 crabs per pot (33.6%). These percentages are nearly identical and no statistically significant difference exists among them (p = 0.99).

The percent of the total annual catch made at each station ranged from 26 to 38% at Kenwood Beach, from 23 to 39% at the Plant Site, and from 30 to 45% at Rocky Point (Figure 5). The mean number of crabs caught per pot by station has shown no meaningful change between pre-operational and operational periods. The overall weighted pre-operational mean for all stations combined was 4.24 crabs per pot, whereas the weighted operational mean was 6.25 crabs per pot (4.35 if 1981 data are excluded). If 1968 data are also excluded, the pre-operational average becomes 4.52 crabs per pot. Thus, the elimination of the most- and least-productive years yields similar long-term mean catches. During the pre-operational period Kenwood Beach averaged 4.15 crabs per pot (32.6%), the Plant Site averaged 4.12

crabs per pot (32.4%), and Rocky Point averaged 4.46 crabs per pot (35.0%). Since 1975, these same stations produced 6.24 (33.3%), 6.37 (34.0%), and 6.15 (32.8%) crabs per pot, respectively; the percentages were essentially unchanged from the pre-operational period.

Figure 6a illustrates the 14-year mean seasonality of the crab populations by station and the similarity between these three stations. Catches were generally small in May, as a result of cool water temperatures (14 to 18°C) which prevented full activity of the crabs. With rising water temperatures, catches increased steadily until August when they approached seven crabs per pot. A decline at all stations was observed for September followed by a second peak in October. The September decline resulted from a sharp decrease in the number of males only (Figure 6b), while females continued to increase in numbers until the October peak was reached. Decreasing water temperatures during November and December reduced crab activity and brought about a rapid decline in catch size.

The October peak reflected migrating females as they moved through the area on their way to higher salinity water of the lower bay for eventual spawning. Females normally spawn at salinities of 22 to 28 ppt (Sandoz and Rogers 1944, Newcombe 1945) which larvae need to survive. Costlow and Bookhout (1959) observed normal hatching at salinities as low as 20.1 ppt with all larvae hatching as first-stage zoeae and no prezoeae were observed. At lower salinities, however, larvae that hatch do so as prezoeae and do not survive (Sandoz and Rogers 1944). Although spawning is uncommon in the Calvert Cliffs area and although Truitt (1939) stated that sponge crabs (female with egg pad) are seldom seen north of the Rappahannock River in Virginia (about 80 km down-bay from the CCNPP)
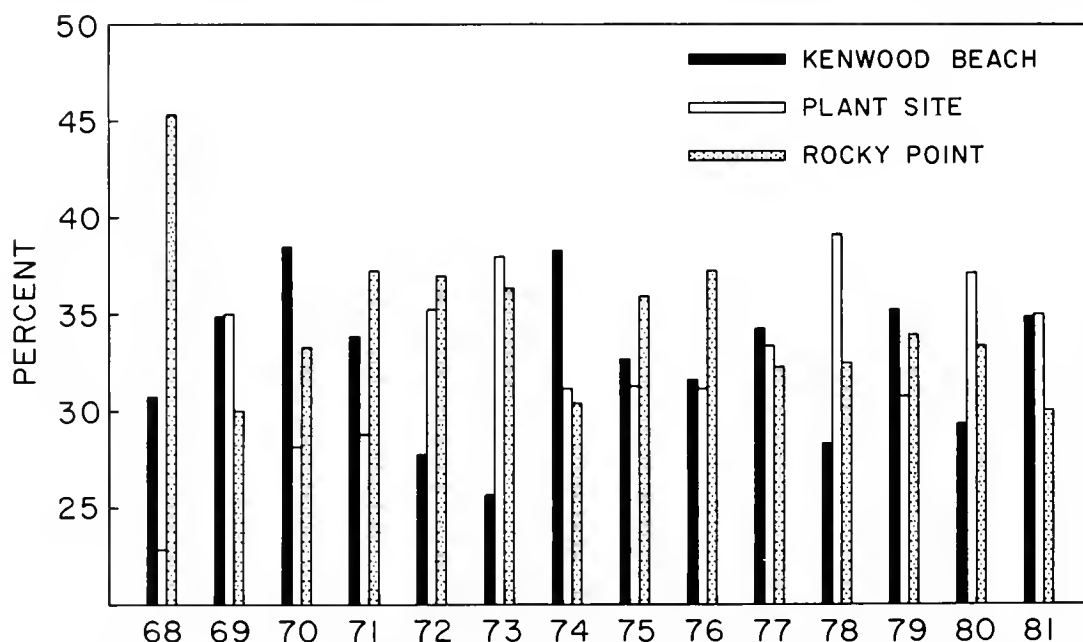

Figure 5. Percent of annual catch made at each station from 1968 to 1981 based on catch per pot.

TABLE 3.

Numbers and weights (kg) of caught blue crabs, number of pots fished, and number of crabs caught per pot
at three stations in mid-Chesapeake Bay from 1968 to 1981.

| Year	Males		Females		Number of Pots Fished	Number of Crabs per Pot
	Number	Weight	Number	Weight		
KENWOOD BEACH						
1968	57	11	24	4	99	0.82
1969	677	88	296	37	156	6.24
1970	381	62	205	26	192	3.05
1971	905	143	673	87	246	6.41
1972	537	84	289	37	265	3.12
1973	573	113	200	28	303	2.55
1974	996	184	562	86	276	5.64
1975	834	130	769	111	303	5.29
1976	406	56	476	65	275	3.21
1977	388	84	312	51	249	2.81
1978	491	82	461	73	284	3.35
1979	957	156	1,054	149	291	6.91
1980	527	106	487	81	283	3.58
1981	2,618	339	2,562	341	293	17.68
Totals	10,347	1,639	8,370	1,174	3,515	5.32
PLANT SITE						
1968	39	8	18	3	96	0.59
1969	720	96	270	34	156	6.35
1970	212	31	183	27	180	2.19
1971	777	117	630	84	257	5.47
1972	602	94	474	60	265	4.06
1973	644	104	580	79	325	3.77
1974	743	121	468	63	264	4.59
1975	827	138	708	103	300	5.12
1976	409	57	482	63	283	3.15
1977	348	69	360	60	254	2.79
1978	630	102	757	111	305	4.55
1979	1,002	150	776	108	295	6.03
1980	475	90	830	145	289	4.52
1981	2,495	311	2,813	373	300	17.69
Totals	9,923	1,489	9,349	1,314	3,569	5.40
ROCKY POINT						
1968	62	14	39	7	86	1.17
1969	598	78	272	35	160	5.44
1970	321	52	191	30	192	2.67
1971	975	157	832	122	257	7.03
1972	655	99	484	74	265	4.30
1973	536	77	526	78	270	3.93
1974	627	95	574	81	269	4.46
1975	720	116	1,044	149	299	5.90
1976	430	59	642	92	283	3.79
1977	344	64	337	54	253	2.69
1978	586	100	551	83	297	3.83
1979	1,075	172	876	129	293	6.66
1980	462	85	712	131	289	4.06
1981	1,740	212	2,878	396	303	15.24
Totals	9,131	1,381	9,958	1,461	3,516	5.43
ALL STATIONS COMBINED						
1968	158	33	81	15	281	0.85
1969	1,995	262	838	106	472	6.00
1970	914	145	579	83	564	2.65
1971	2,657	417	2,135	293	760	6.31
1972	1,794	277	1,247	171	795	3.83
1973	1,753	295	1,306	185	898	3.41
1974	2,366	400	1,604	230	809	4.91
1975	2,381	384	2,521	364	902	5.43
1976	1,245	172	1,600	220	841	3.38
1977	1,080	217	1,009	165	756	2.76
1978	1,707	285	1,769	267	886	3.92
1979	3,034	478	2,706	386	879	6.53
1980	1,464	281	2,029	357	861	4.06
1981	6,853	863	8,253	1,110	896	16.86
Totals	29,401	4,509	27,677	3,949	10,600	5.38
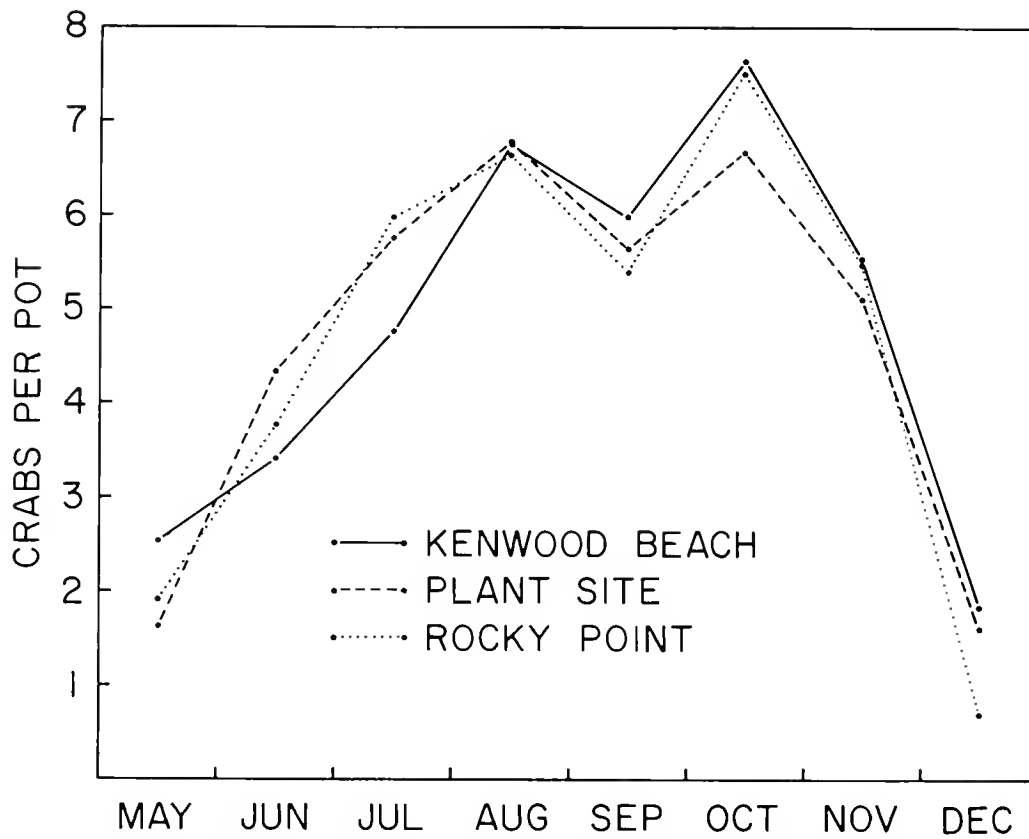
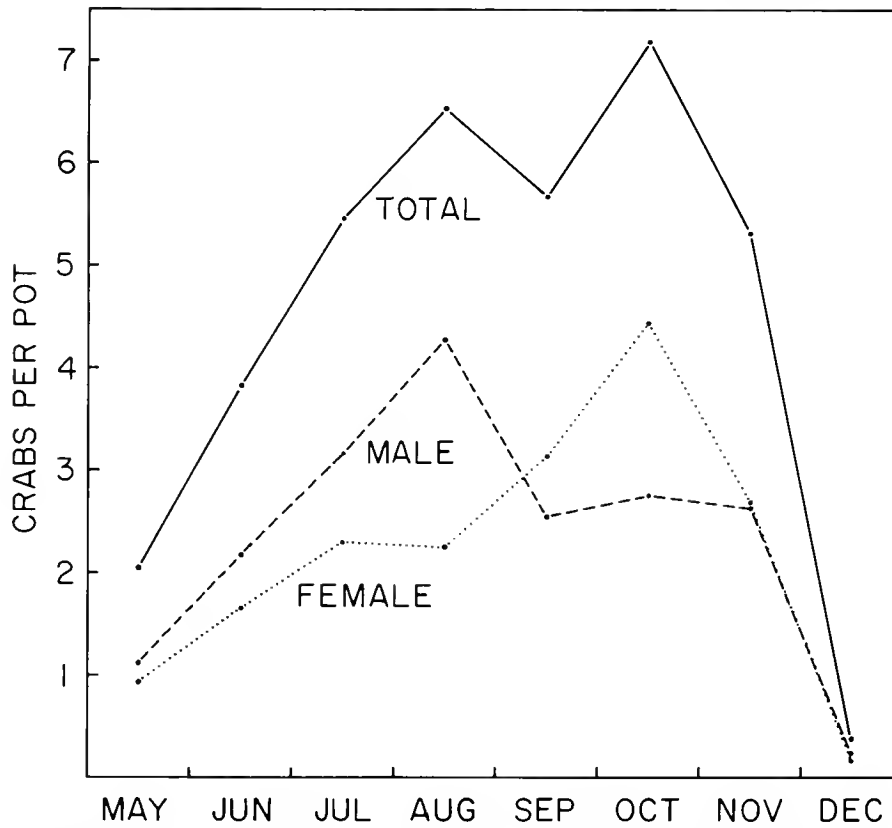Figure 6a. Monthly catch per pot by station showing the similiary between stations.

Figure 6b. Monthly catch per pot by sex showing the difference in peak abundance for males and females.

except during dry years, some are occasionally seen. From 1968 to 1979, 59 sponge crabs were caught (0.34% of all females). During the dry years of 1980 and 1981, however, 64 were collected (0.62% of all females). Salinity (20 to 21 ppt) and temperature (24 to 25°C) combinations in late August and early September 1981 were high enough in the study area for successful hatching although no evidence of this was observed. Hatching this far north in the bay would have been extremely unusual because even a blue crab megalops in this area of the Chesapeake is rare (Cargo 1960).

Annual percentages of males are plotted by station in Figure 7a. When stations are averaged within years, the annual percentages show a decline from 66% in 1968 to 45% in 1981. The highest percent males occurred in 1969 (70%) and the lowest occurred in 1980 (42%). Analysis of covariance revealed a significant decrease in percent males since 1968 ($p < 0.001$). The analysis detected no difference in the rate of decrease between stations ($p > 0.99$); thus it has occurred equally at all stations (Figure 7b). This decrease in percent males might be easily explained had a long-term increase in salinity been evident during this time, but Figure 8 shows no increase in salinity; the regression line is not significantly different from a no-slope line ($p = 0.56$). Thus, the reasons for the decrease in male/female ratios are not understood, nor are the implications of this decline to a fishery in which females are worth considerably less than males. Because choice male crabs are destined for crab houses and restaurants to be eaten steamed, while females and small or light males go primarily to processing plants to be picked, the choice males may be worth two to three times more than females during much of the season. If this decline in percent males is more widespread than the Calvert Cliffs area, such a decline could result in economic losses to crabbers and others dependent on the fishery.
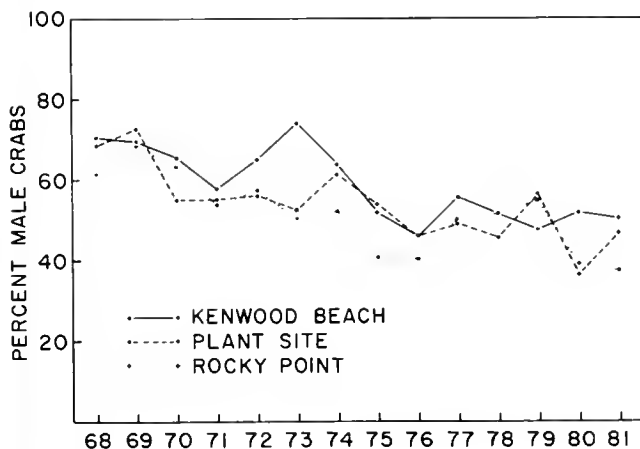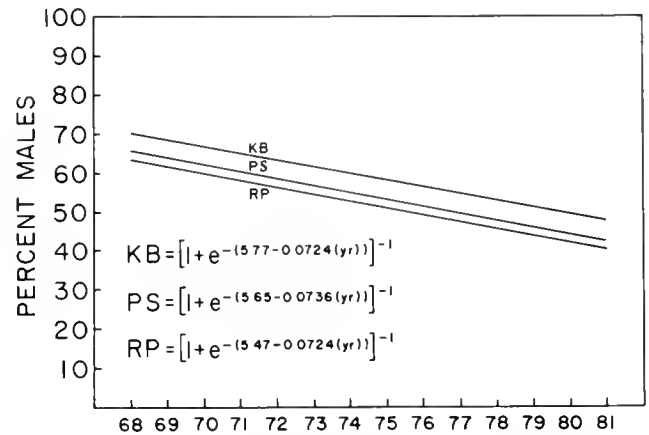

Figure 7b. Curves resulting from analysis of covariance model fitted to logit-transformed proportions of males at three stations showing the decline in percent males and the similarity in rates of decline.

$$KB = \left[1 + e^{-(5.77 - 0.0724(yr))}\right]^{-1}$$
$$PS = \left[1 + e^{-(5.65 - 0.0736(yr))}\right]^{-1}$$
$$RP = \left[1 + e^{-(5.47 - 0.0724(yr))}\right]^{-1}$$

$$y = 4.60 + 0.11x$$
$$r^2 = 0.03$$
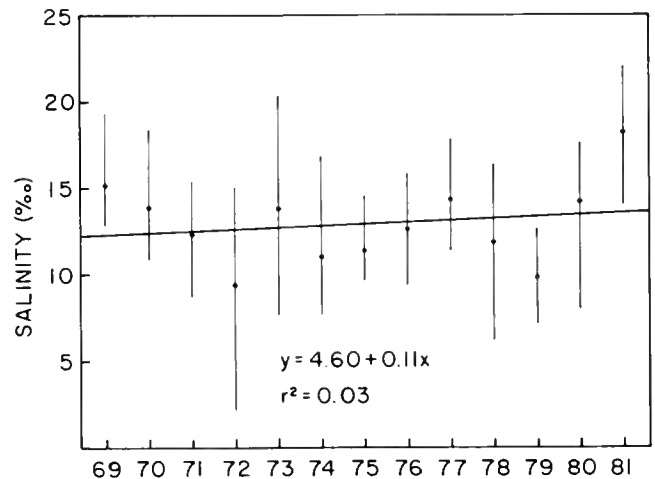
Figure 8. Annual mean salinity in the Calvert Cliffs area from 1968 to 1981 showing the absence of any long-term trend. Vertical bars represent annual salinity ranges.

Poor catches and/or dead crabs in pots were occasionally observed during July and August as a result of low-dissolved oxygen concentrations. Although uncommon at all stations, these episodes occurred more often at Kenwood Beach than elsewhere because of bathymetric differences. The bottom at Kenwood Beach sloped from a 3- to 10-m depth more gradually than at the Plant Site or Rocky Point allowing anoxic water to upwell after westerly winds moved surface waters offshore. These incidents usually lasted from 1 to 3 days when oxygen concentrations ranged from just under 3.0 to 0.1 mg/ℓ. Fish trapped in pots generally were dead and crabs were dead or nearly so. Although catches at Kenwood Beach were much reduced during these times, the overall reduction for the season compared to other stations

Figure 7a. Annual percent of catch consisting of males at the three stations from 1968 to 1981.

was minimal. May (1973) described similar occurrences in Mobile Bay, Alabama, and discussed the responsible conditions. He stated that one of the best indexes of the extent of oxygen depletion was the mortality of fish and crabs caught in pots.

Abundance, size, and sex ratio data indicated no special attraction of crabs to the Plant Site station. Crabs were attracted by warm water at the P. H. Robinson Generating Station in Galveston Bay, Texas, during the cooler seasons and by the entrainment of small fish (Gallaway and Strawn 1975).

An estimated 4.76×10^6 crabs were impinged on the rotating screens at Calvert Cliffs from 1975 to 1981. The estimate of 3.8×10^5 in 1980 (Hirshfield et al. 1981) was similar to the 1975—78 mean of 4.0×10^5; however, it was well below the 1.12×10^6 and 1.66×10^6 for 1979 and 1981, respectively (Hirshfield et al. 1980, Hirshfield and Hixson 1982). Annual impingement estimates were correlated with the annual mean number of crabs caught per pot from all stations combined ($r^2 = 0.83$). Although the number of impinged crabs was large (6.8×10^5 annual mean for 1975—81), it was much lower than the estimate of 1.95×10^6 crabs per year for 1976—77 at the Chalk Point Steam Electric Station on the Patuxent River, Maryland (Academy of Natural Sciences of Philadelphia

1983). The impingement of crabs and their subsequent wash-off from the screens at the CCNPP had virtually no affect on survival which exceeded 99% (Burton 1976).

Differences among years were detected for all population variables examined and variation among stations over time was moderate, but other than slightly larger males at Kenwood Beach than at the other stations and a higher percentage of males at Kenwood Beach than at Rocky Point, no statistically significant station differences were detected during pre-operational or operational periods. Perhaps one of the most significant findings of this study, however, was the long-term decrease in the percent of males that occurred equally among stations. All year-to-year changes in population structure, whether significant or not, appeared to be natural fluctuations and unrelated to operation of the CCNPP.

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MOVEMENTS OF TAGGED MALES OF TANNER CRAB
CHIONOECETES BAIRDI RATHBUN OFF
KODIAK ISLAND, ALASKA

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ABSTRACT   From 1973 through 1978, 11,196 males of the Tanner crab *Chionoecetes bairdi* Rathbun were tagged and released off of Kodiak Island, Alaska. A total of 1,961 tags was returned, 1,404 with accurate recovery data. Males which were tagged in bays tended to move into offshore areas while those tagged offshore remained in that general area. Crab movements were not extensive; mean net movement for all recoveries was 24 km (15 miles). The generalized movement models indicate the presence of stocks of large male Tanner crabs in the Shelikof, Marmot-Chiniak, Eastside, and Southwest areas of Kodiak Island.

KEY WORDS   Tanner crabs, *Chionoecetes bairdi*, migration, tagging, movement

INTRODUCTION

The Tanner crab *Chionoecetes bairdi* Rathbun occurs from shallow nearshore areas to depths of 473 m (259 fm) and ranges from Puget Sound, Washington (Slipp 1952) and the Oregon coast (Hosie 1974) to the Aleutian Islands and southeastern Bering Sea (Garth 1958) where male Tanners are the basis for a major fishery (Otto 1981).

Many fishermen hold traditional beliefs concerning Tanner crab migrations and cite time-related changes in catch with depth as evidence of inshore-offshore movement. Prior to this study, movement patterns of *C. bairdi* were unknown; however, some information on migrations of congeneric species does exist. Migration of the snow crab *C. opilio (O. fabricius)* was studied in the Atlantic around the Gaspé region of the Gulf of Saint Lawrence by Watson (1970) and Watson and Wells (1972). Their results indicated that tagged males traveled relatively little, with 85% of the returns recaptured within 20.3 km (11 mi) of the release points. Katoh et al. (1956) and Yoshida (1941) observed bathymetric separation of the sexes of *C. opilio* in the Sea of Japan indicating at least a seasonal migration for mating. Pereyra (1967) concluded that males of *C. tanneri* off the coast of Oregon showed seasonal variations in relative abundance with depth, whereas the female population was fairly stationary during all seasons, thus suggesting movement of males for reproductive purposes.

In recent years, the fishery for *C. bairdi* has developed exponentially, but data on the life history of this species have not been accumulated in like manner. While *C. bairdi* has accounted for about one fourth of the recent domestic harvest of crabs by U.S. fishermen (Donaldson 1980), resource data are insufficient to define discrete stocks in most areas. The purpose of this study was to determine whether migrations or displacement of aggregations of males of *C. bairdi* occur over the shelf region surrounding Kodiak Island.

MATERIALS AND METHODS

Migration was studied by the release and recapture of tagged male crabs during a 6-year period (1973–1979). Males of ≥ 110 mm carapace width (CW) were tagged and released between July 1973 and August 1975 off Kodiak Island, AK. In 1976, minimum tagging size was raised to 135 mm CW because of the establishment of a commercial, minimum size limit.

Crabs were tagged with a combination of Floy disc, FD 67 "T" bar, and a modified FD 67 "T" bar (also known as the McBride tag). The Floy disc is a temporary tag which is lost during ecdysis. The FD 67 "T" bar and modified FD 67 "T" bar are prototype permanent tags. Floy disc tags were used in all years except 1977; both FD 67 "T" bars and Floy discs were used in 1975; and only the modified 67 "T" bar was used in 1977.

Crabs were captured with 2.1- × 2.1-m (7- × 7-ft) crab pots which were covered with 89-mm (3.5-in.) mesh. Tag number, date, location, and depth of capture were recorded for crabs tagged from 1973 through 1975. Exoskeletal age (intermolt period) and carapace width were also recorded beginning in 1976. Females, generally, are too small to be captured in pots and none were tagged during this study.

Crabs were captured, tagged, and released at various inshore (bay) and offshore locations (Figure 1). Tagged crabs were recovered from fishermen and at processing plants. Recovery data included tag number, date, location and depth of capture, carapace width, and exoskeletal age. Only recaptures with complete recovery data were used in this study.

Distance and direction of net migration and the absolute depth change were recorded for the year of release and for inshore (bay) and offshore areas. All recovery data were collated by specific geographical area for the duration of the study and migration by specific areas was analyzed. The data were insufficient to assess migration by cohorts;
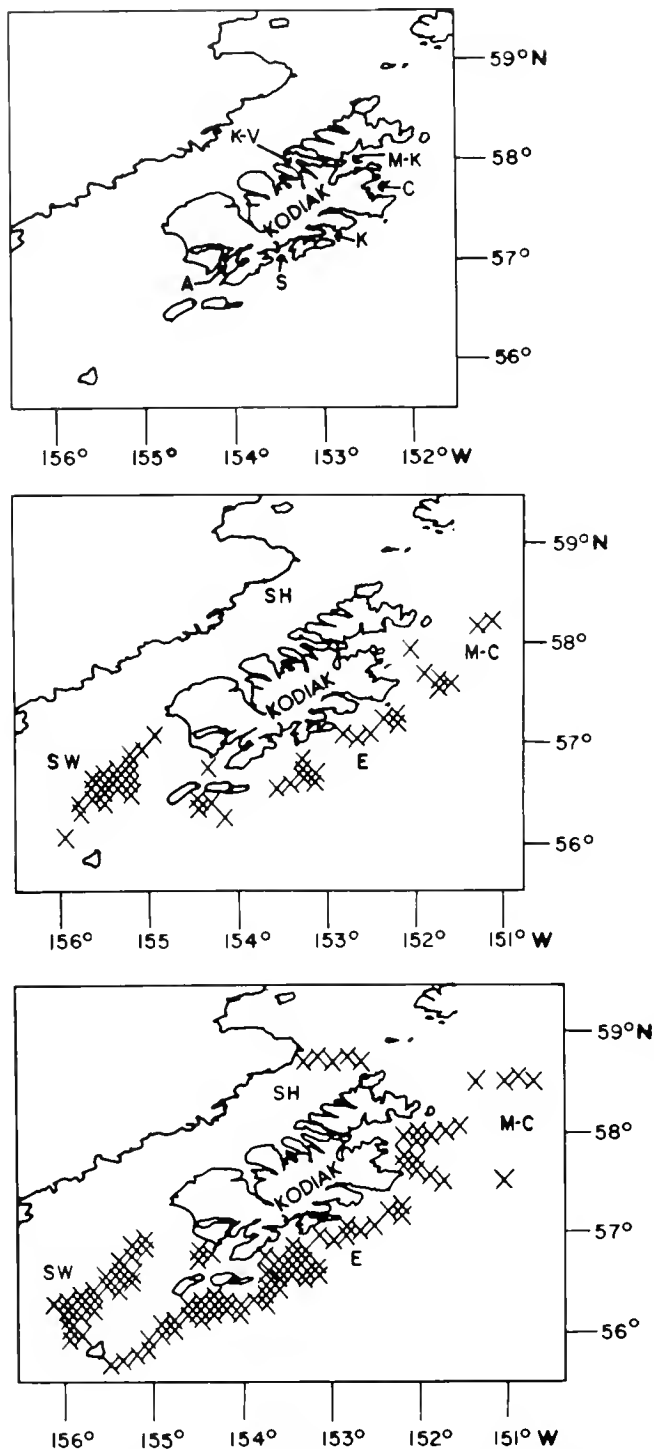
Figure 1. Release sites of males of the Tanner crab *Chionoecetes bairdi* Rathbun at Kodiak, AK. Top: bay sites (∕) 1973–1978. Middle: offshore sites (×) 1973–1975. Bottom: offshore sites (×) 1976–1978. Afitak Bay (A), Chiniak Bay (C), Eastside area (E), Kiliuda Bay (K), Kupreanof-Viekoda Bay area (K-V), Marmot-Chiniak Bay area (M-C), Marmot-Kizhuyak Bay area (M-K), Sitkalidak Bay (S), Shelikof area (SH), Southwest area (SW).

therefore, the crabs were grouped by 30-day periods between release and recovery. The mean movement by each

such group was determined. Changes in depth were determined and represent the percentage of crabs that were recovered deeper, shallower, or remained at the release depth. Directions of movement and recovery locations were analyzed using computer-calculated ellipses that represented a 95% confidence interval of direction and recovery region data. Information on the distribution of fishing effort was obtained from a fish-ticket reporting system.

RESULTS

1973

A total of 2,285 male crabs (⩾ 110 mm CW) were tagged and released between 15 July and 5 August (Table 1). The majority (2,024) was released in offshore areas, while 261 tagged crabs were released in inshore bays. A total of 486 recoveries were made, 415 from offshore and 71 from inshore (bays). Catch data were available from 361 (15.8%) of the tagged crabs. Time of freedom ranged from 26 to 1,376 days (Table 2). Crabs recovered within one, two, and three years of release represented 72.5%, 19.1%, and 7.4% of total recoveries, respectively. Three crabs (0.8%) were captured in their fourth year after tagging. Mean migration distance (based on two or more recovered crabs) ranged from 49.6 km (30.8 mi) for nine crabs that were free between 961 and 990 days, to 11.5 km (7.1 mi) for two crabs that were free 481 to 510 days (Table 2). The mean absolute distance traveled was 27.9 km (17.3 mi) for all recovered crabs. Crabs that were tagged and released in bays tended to move offshore while those tagged and released offshore remained offshore and within the geographic area of release. Depth change was variable, with 175 crabs (48.4%) recaptured at points shallower than their release depth, 179 (49.6%) recaptured at deeper points, and 7 (1.9%) recaptured at their release depth.

1974

During 1974, 1,846 male crabs (⩾ 110 mm CW) were tagged with Floy disc tags and released (Table 1). The majority (1,472) was released in offshore areas, while 374 were released in bay areas. A total of 397 tags were recovered (340 offshore, 57 inshore). Catch data were available from 310 recoveries or 16.8% of all crabs tagged. Time of freedom ranged from 30 to 1,080 days (Table 2). Crabs recaptured within one, two, and three years of release represented 57.7%, 36.9% and 5.4% of all recoveries, respectively. The longest mean (absolute) movement was 83.5 km (51.9 mi) for four crabs that were free between 991 and 1,020 days; the shortest mean movement was 12.0 km (7.5 mi) for two crabs that were free from 1,021 to 1,050 days (Table 2). The overall mean distance of net migration was 26.8 km (16.7 mi). Movement in all offshore areas was localized within the area of release. Crabs tagged and released in bays tended to move offshore as did the

TABLE 1.

Number of tagged males of the Tanner crab *Chionoecetes bairdi* Rathbun released and recovered off Kodiak Island, AK, 1973–1978.

Tagging Dates	Number Released Inshore	Number Recoveries	Usable Recoveries	% of Releases Usable	Number Released Offshore	Number Recoveries	Usable Recoveries	% of Releases Usable	Total Released	Total Recovered	Total Usable Recoveries	% of Releases Usable
15 Jul – 5 Aug 1973	261	71	51	19.5	2,024	415	310	15.3	2,285	486	361	15.8
28 Jun – 26 Jul 1974	374	57	38	10.2	1,472	340	272	18.5	1,846	397	310	16.8
15 Jul – 27 Jul 1975	430	68	52	12.1	502	142	72	14.3	932	210	124	13.3
8 Nov – 12 Nov 1975[1]	408	31	22	5.4	766	84	58	7.6	1,174	115	80	6.8
24 Jun – 1 Aug 1976	301	65	38	12.6	2,023	434	280	13.8	2,324	499	318	13.7
27 Jun – 18 Aug 1977	321	14	11	3.4	1,351	167	147	10.9	1,672	181	158	9.4
9 Jul – 13 Nov 1978	0	—	—	—	963	73	53	5.5	963	73	53	5.5
Totals	2,095	306	212	10.1	9,101	1,655	1,192	13.1	11,196	1,961	1,404	12.5

[1] FD 67 "T" tags

TABLE 2.

Distance moved from release site for males of the Tanner crab *Chionoecetes bairdi* Rathbun off Kodiak Island, AK, 1973–1978.
Mean movement from release site in km and number of crabs indicated within parentheses.

Days of Freedom	1973		1974		1975* ADFG		1975* NMFS		1976		1977		1978		All Years	
1– 30	23.7	(3)	17.1	(1)	— —	(0)	— —	(0)	— —	(0)	— —	(0)	— —	(0)	23.5	(4)
31– 60	24.0	(3)	24.8	(17)	7.3	(3)	— —	(0)	— —	(0)	11.4	(2)	6.0	(1)	20.9	(26)
61– 90	11.0	(1)	22.7	(6)	8.0	(1)	— —	(0)	— —	(0)	9.8	(5)	87.0	(1)	20.8	(14)
91– 120	31.6	(23)	25.0	(1)	— —	(0)	— —	(0)	— —	(0)	9.7	(7)	— —	(0)	26.0	(31)
121– 150	35.3	(12)	60.0	(1)	15.4	(22)	— —	(0)	— —	(0)	32.3	(4)	— —	(0)	24.4	(39)
151– 180	17.9	(21)	— —	(0)	19.4	(9)	— —	(0)	17.5	(9)	15.3	(11)	19.0	(1)	17.2	(51)
181– 210	26.9	(21)	— —	(0)	17.4	(20)	— —	(0)	18.4	(46)	17.7	(38)	19.5	(4)	19.5	(129)
211– 240	30.8	(39)	— —	(0)	16.0	(26)	— —	(0)	18.5	(57)	15.9	(34)	17.3	(27)	20.1	(183)
241– 270	27.9	(106)	43.3	(24)	12.3	(19)	— —	(0)	23.0	(59)	24.0	(47)	18.4	(19)	25.8	(274)
271– 300	22.3	(33)	28.6	(78)	20.6	(5)	— —	(0)	25.8	(38)	— —	(0)	— —	(0)	26.3	(154)
301– 330	— —	(0)	19.1	(48)	— —	(0)	— —	(0)	46.0	(1)	— —	(0)	— —	(0)	19.6	(49)
331– 360	— —	(0)	14.3	(4)	— —	(0)	— —	(0)	— —	(0)	— —	(0)	— —	(0)	14.3	(4)
One Year																
361– 390	— —	(0)	— —	(0)	— —	(0)	— —	(0)	10.0	(1)	— —	(0)	— —	(0)	10.0	(1)
391– 420	24.7	(8)	— —	(0)	4.0	(1)	30.0	(1)	— —	(0)	— —	(0)			23.2	(10)
421– 450	12.8	(4)	25.2	(4)	32.0	(1)	38.1	(2)	— —	(0)	47.0	(1)			28.8	(12)
451– 480	— —	(0)	19.6	(5)	— —	(0)	25.5	(30)	14.0	(2)	— —	(0)			24.1	(37)
481– 510	11.5	(2)	24.0	(2)	— —	(0)	14.9	(36)	39.5	(2)	— —	(0)			17.7	(42)
511– 540	56.0	(1)	38.5	(14)	— —	(0)	15.8	(5)	9.3	(3)	40.5	(2)			25.7	(25)
541– 570	— —	(0)	20.3	(19)	20.5	(4)	— —	(0)	8.5	(1)	20.0	(2)			19.9	(26)
571– 600	— —	(0)	24.8	(12)	25.4	(8)	— —	(0)	26.0	(11)	25.5	(2)			25.4	(33)
601– 630	31.7	(3)	24.0	(25)	20.5	(2)	— —	(0)	29.0	(60)	20.7	(3)			26.8	(93)
631– 660	23.2	(29)	24.3	(34)	41.0	(1)	— —	(0)	23.0	(21)	— —	(0)			23.8	(85)
661– 690	30.8	(21)	— —	(0)	— —	(0)	— —	(0)	— —	(0)	— —	(0)			30.8	(21)
691– 720	13.0	(1)	— —	(0)	— —	(0)	— —	(0)	— —	(0)	— —	(0)			13.0	(1)
Two Years																
721– 750	— —	(0)	— —	(0)	— —	(0)	— —	(0)	— —	(0)	— —	(0)			— —	(0)
751– 780	— —	(0)	— —	(0)	— —	(0)	— —	(0)	— —	(0)					— —	(0)
781– 810	31.7	(3)	— —	(0)	— —	(0)	21.0	(4)	— —	(0)					25.6	(7)
811– 840	49.0	(1)	19.0	(1)	— —	(0)	— —	(0)	— —	(0)					34.0	(2)
841– 870	29.0	(2)	— —	(0)	— —	(0)	15.0	(2)	— —	(0)					19.5	(4)
871– 900	— —	(0)	— —	(0)	— —	(0)	— —	(0)	— —	(0)					— —	(0)
901– 930	17.0	(1)	— —	(0)	138.0	(1)	— —	(0)	31.0	(1)					62.0	(3)
931– 960	23.5	(2)	41.3	(3)	55.0	(1)	— —	(0)	41.0	(3)					38.8	(9)
961– 990	49.6	(9)	29.5	(4)	— —	(0)	— —	(0)	28.5	(2)					41.4	(15)
991– 1020	43.1	(7)	83.5	(4)	— —	(0)	— —	(0)	34.0	(1)					55.8	(12)
1021– 1050	38.5	(2)	12.0	(2)	— —	(0)	— —	(0)	— —	(0)					25.3	(4)
1051– 1080	— —	(0)	30.0	(1)	— —	(0)	— —	(0)	— —	(0)					30.0	(1)
Three Years																
1343– 1376	34.3	(3)	— —	(0)	— —	(0)	— —	(0)							34.3	(3)
N	361		310		124		80		318		158		53		1404	
Σ km/N = mean (km)	27.9		26.8		18.2		21.1		23.1		19.4		19.0		24.0	

*ADFG, Alaska Department of Fish and Game; NMFS, National Marine Fisheries Service.

1973 releases. Of the 310 returns, 168 (54.2%) were recovered at points deeper than their release depth, 108 (34.8%) were recovered at shallower points, and 34 (10.9%) were recaptured at their release depth.

1975

Between 15 July and 12 November 1975, 2,106 crabs (≥ 110 mm CW) were tagged and released (Table 1); of these,

1,174 were tagged with FD 67 "T" bar tags and 932 crabs bore Floy discs. A total of 1,268 (60.2%) crabs were released in offshore areas while 838 (39.8%) were released in bays (inshore). A total of 325 were recovered, 226 from offshore and 99 from inshore areas. Catch data are available from 204 of the recoveries or 9.7% of all crabs tagged. Time of freedom ranged from 40 to 935 days (Table 2). Crabs recovered within one, two and three years of release

accounted for 48.8%, 47.4%, and 3.8% of all recoveries, respectively. The longest mean net movement was 38.1 km (23.6 mi) for two crabs that were free from 421 to 450 days (Table 2). The shortest mean movement was 7.3 km (4.5 mi) for three crabs that were free from 31 to 60 days. The overall mean distance of migration was 19.3 km (12.0 mi). Little difference existed in the mean (absolute) distances of migration for crabs tagged with the FD 67 "T" bar (21.1 km [13.1 mi]) versus those bearing Floy discs (18.2 km [11.3 mi]). Recoveries were restricted to the northeastern and eastern sides of the island. Movement of offshore crabs was localized around the area of release while crabs tagged inshore moved offshore. Forty-one (20.1%) crabs were recaptured at points shallower than their release, 153 (75.0%) were recaptured at deeper points, and 10 (4.9%) were recaptured at their release depth.

1976

Between 24 June and 8 August 1976, 2,324 crabs (≥ 135 mm CW) were released bearing Floy disc tags. As in previous years, the majority of tagged crabs (2,023 [87%]) were released in offshore areas; 301 (13%) were tagged and released inshore (bays) (Table 1). A total of 499 recoveries were made of which 434 were crabs tagged and released offshore and 65 were crabs that had been tagged and released inshore. Catch data are available from 318 recoveries or 13.7% of the total releases. Time of freedom ranged from 166 to 994 days (Table 2). Crabs recovered within one, two, and three years of release represented 66.3%, 31.5% and 2.2%, respectively, of total recoveries. Mean movement by 30-day periods ranged from 9.3 km (5.8 mi) for three crabs that were free from 511 to 540 days to 41.0 km (25.5 mi) for three crabs that were free from 931 to 960 days. The mean (absolute) distance traveled by all 318 crabs was 23.1 km (14.4 mi) (Table 2). Two-hundred nine crabs (65.7%) were recovered from points shallower than release depth and 109 (34.3%) were recovered from water deeper than release depth.

1977

Between 27 June and 18 August 1977, 1,672 crabs (≥ 135 mm CW) were tagged with the modified FD 67 "T" bar tag; 1,351 (80.8%) were released in offshore areas, while 321 (19.2%) were released in bays. A total of 181 tags were recovered (167 offshore, 14 inshore). Catch data are available from 158 or 9.4% of the total releases. Time of freedom ranged from 44 to 617 days (Table 2). The majority of the recoveries (148 [93.7%]) occurred within one year of release, the remainder (10 [6.3%]) were recovered during the second year. Mean movement ranged from 9.7 km (6.0 mi) for seven crabs that were free from 91 to 120 days to 40.5 km (25.2 mi) for two crabs that were free 511 to 540 days. The mean (absolute) distance migrated for all 158 crabs was 19.4 km (12.1 mi) (Table 2). Movement patterns were consistent with those from previous years

and regions where tagging took place. The majority of crabs (105 [66.5%]) were recovered from points shallower than their release sites, 43 (27.2%) had moved deeper, while 10 (6.3%) were recaptured at their release depth.

1978

A total of 963 crabs (≥ 135 mm CW) were tagged with Floy disc tags and released in the southern portion of the Kodiak Island area. No tagging was done in bays. Seventy-three recoveries were made; reliable catch data are available for 53 or 5.5% of the total releases. Time of freedom ranged from 55 to 263 days (Table 2). The longest mean (absolute) movement was 19.5 km (11.8 mi) (Table 2). No crabs tagged offshore were recovered inshore. Thirty-seven crabs (71.2%) were recovered in depths shallower than release depths, 15 (28.8%) were recovered at deeper depths, and 1 crab was recaptured at the same depth as released.

Inshore Areas, 1973–1978

Tagging and recovery trends for inshore (bay) areas for all years combined are depicted in Figure 2. A total of 212 tagged crabs with recovery data from all bays (Table 1) were obtained during the course of this study; they ranged from 52 crabs from Sitkalidak Bay (S) to 17 from the Marmot-Kizhuyak Bay area (M-K). Movement from the midpoint of the release locations to the midpoint of the recovery locations was greatest in Marmot-Kizhuyak Bay (33.6 km [20.9 mi]), while the least movement occurred in the Kupreanof-Viekoda Bay (K-V) area (9.6 km [6.0 mi]). Movement of crabs tagged and released in Kiliuda (K) and Alitak (A) bays averaged 14.4 km (8.9 mi); Chiniak Bay (C) movement averaged 17.6 km (10.9 mi); and Sitkalidak Bay on the southeastern side of Kodiak Island averaged 22.3 km (13.9 mi). All crabs tagged and released in bays demonstrated an offshore movement with the exception of Kupreanof-Viekoda Bay area recoveries, which demonstrated both offshore and onshore movement.

Offshore Areas, 1973–1978

Of the tagged crabs released in offshore areas from 1973 to 1978, 1,192 were recovered with complete catch data (Table 1). Direction and magnitude of migration are depicted in Figure 2. Four individual stocks are somewhat apparent on that figure: (1) Marmot-Chiniak (M-C) area, 230 tags recovered; (2) Eastside (E), 494 tags recovered; (3) Southwest (SW), 453 tags recovered; and (4) Shelikof (SH), 15 tags recovered. Crabs appeared to move around in the area of tagging and release with no immigration into bay areas or adjacent stocks. There is an apparent westerly movement of crabs released in the northern portion of the Eastside and Shelikof areas; however, because of the small number of tagged crabs recovered, the data do not permit a firm conclusion. The apparent northerly movement in the southern portion of the Eastside area was probably caused by a lack of commercial fishing to the south of the release points.

The Marmot-Chiniak and Eastside stocks are separated by a deep gully of 144 to 215 m (80 to 120 fm) depth; that gully may be a physical barrier that separates postlarval crabs into independent stocks. Likewise, the Eastside and Southwest stocks are separated by a large shallow area of 18 to 36 m (10 to 20 fm) running northeast-southwest; that ridge may also limit or cross channel movement.
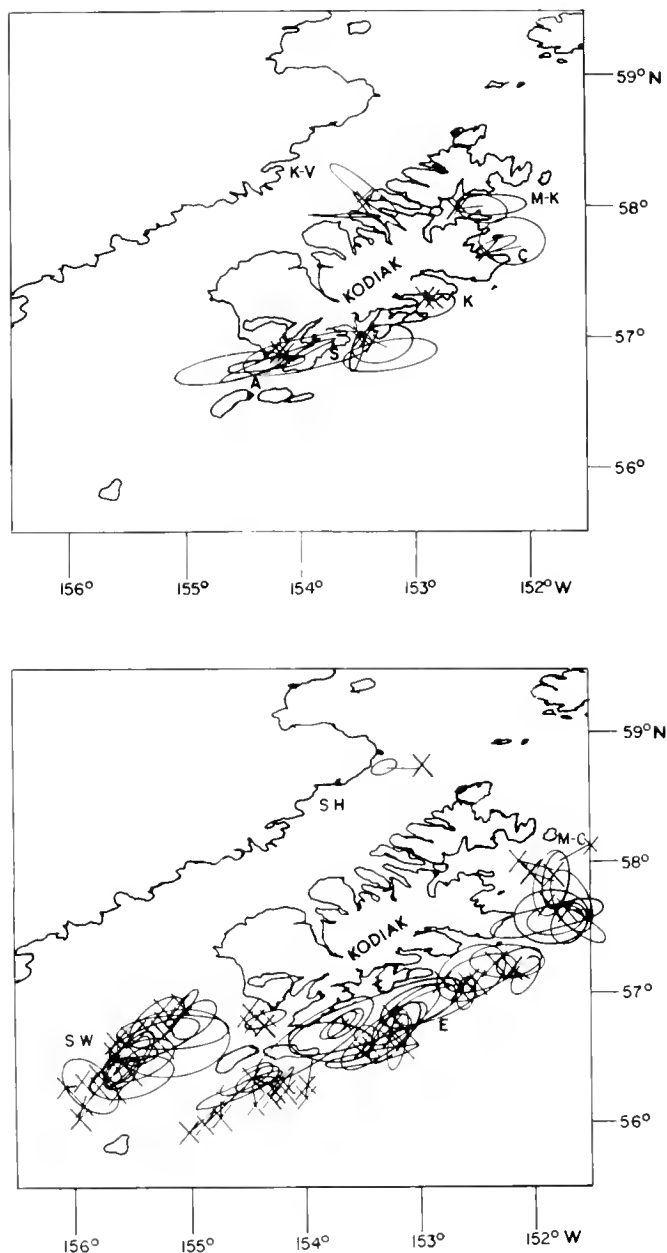

Figure 2. Movements of tagged males of the Tanner crab *Chionoecetes bairdi* Rathbun released from 1973 through 1978 at Kodiak, AK. Top: inshore (bay) recoveries (212). Bottom: offshore recoveries (1,192). (Ellipse represents 95% confidence region.) Atitak Bay (A), Chiniak Bay (C), Eastside area (E), Kiliuda Bay (K), Kupreanof-Viekoda Bay area (K-V), Marmot-Chiniak Bay area (M-C), Marmot-Kizhuyak Bay area (M-K), Sitkalidak Bay (S), Shelikof area (SH), Southwest area (SW).

DISCUSSION

Tag recovery is dependent on when and where fishermen place their crab pots. From 1973 through 1978, 57,334.7 mt (124,809,323 lb) of Tanner crabs were harvested off Kodiak Island. Those landings represented approximately 49,934,730 crabs at 1.13 kg (2.5 lb) per crab. After release, tagged crags were first subjected to recapture in the fall fishery (August–December) for the king crab *Paralithodes camtschatica* (Tilesuis). (Tanner crabs are captured incidental to king crabs because the two species tend to share the same habitat.) Tagged crabs were then subjected to recapture during the Tanner crab fishery that opens between November and January and closes in April or May.

From 1973 to 1978 fishing effort expanded to cover all major habitats of king and Tanner crabs. Fishermen with smaller vessels tended to fish the nearshore areas while fishermen with larger vessels primarily fished the deeper, offshore areas. The tag-recovery data were influenced by the peculiarities in fishing patterns; however, recovery of tagged crabs appeared to be reasonably well distributed over the study area and should provide a reasonable picture of migration.

Tagged males did not move extensively from their release sites. The results of this study demonstrated that although there were examples of extensive movement for small numbers of crabs, the mean (absolute) movement was only 24.0 km (15.0 mi). Although periods of freedom for tagged individuals varied from less than one month to 3.8 years, no correlation between time and absolute distance migrated was evident. Watson (1970) and Watson and Wells (1972) demonstrated a mean movement of 20.3 km (11 mi) for adult males of *Chionoecetes opilio*. Male Tanner crabs that were captured and tagged in bay areas tended to move to deeper, offshore waters while those captured and tagged in offshore waters remained offshore and migrated randomly within a geographic area. These findings have implications for management of the resource. High exploitation rates in offshore areas may be partially compensated for by immigration of mature crabs from bays. High exploitation rates in bays may present a more difficult management situation because recruitment into the fishable size range is dependent on annual recruits to legal size with no apparent immigration of offshore crabs.

An additional result of this study is that postlarval crabs may be separated into manageable stocks because there is little or no apparent movement between designated geographic regions. Additional tag-and-recapture studies in the vicinity of apparent geographic stock boundaries and bathymetric features should help demonstrate whether or not those apparent stocks are distinct or an artifact of aggregated release locations.

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RESEARCH NOTE

CHEMICAL INDUCTION OF SPAWNING BY SEROTONIN IN THE OCEAN QUAHOG *ARCTICA ISLANDICA* (LINNÉ)

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ABSTRACT   Serotonin injected into the anterior adductor muscle induced spawning in the ocean quahog *Arctica islandica* (Linné) when using either individual or mass spawning techniques. This represents the first successful attempt to induce the release of gametes in this species which historically has been unresponsive to conventional spawning stimuli. The gametes released were competent and fertilization occurred without treating the encapsulated eggs with ammonium hydroxide or other chemicals. Larvae were reared through metamorphosis to early juvenile stage.

KEY WORDS: Ocean quahog, *Arctica islandica*, spawning, serotonin

INTRODUCTION

The ocean quahog *Arctica islandica* (Linné) spawns from August through November on the southern New England shelf and off New Jersey (Jones 1981, Mann 1982). Attempts to spawn the ocean quahog in the laboratory have been unsuccessful. Various combinations of stimuli such as thermal shock, addition of gonadal products, salinity and pH changes, and exposure to hydrogen peroxide, which are effective with many other bivalve species, have not induced spawning (Loosanoff 1953, Landers 1976, Lutz et al. 1982, Mann 1982). All larvae of ocean quahogs cultured to date under laboratory conditions have been reared from stripped gametes that had been fertilized after pretreatment of eggs with ammonium hydroxide (Landers 1976, Lutz et al. 1981).

Serotonin (5-hydroxytryptamine, creatinine sulfate complex) has proven to be an effective chemical inducer of spawning for many bivalve species (Matsutani and Nomura 1982, Gibbons and Castagna [in press]). The injection of serotonin into the anterior adductor muscle or gonad of certain bivalve species when ripe will induce spawning using individual spawning techniques without any additional stimuli. The present study describes the successful spawning of ocean quahogs in the laboratory using serotonin.

MATERIALS AND METHODS

Sexually mature ocean quahogs, ranging in shell length from 8 to 13 cm, were obtained in October 1983 using a

commercial hydraulic dredge in 50 to 80 m of water off Cape May, NJ. The specimens were kept on ice for approximately 12 hours during transport from the sampling site. Upon arrival at the Wachapreague Laboratory of the Virginia Institute of Marine Science, half of the ocean quahogs were immediately placed in individual dishes of seawater for spawning while the other half were held in a recirculating seawater table at 15–16°C.

A 2-mM solution of serotonin (Sigma Chemical Company, St. Louis, MO) was prepared by dissolving crystalline serotonin in 1-μm-filtered seawater. Each ocean quahog was washed and a small notch filed into the valve margin adjacent to the anterior adductor muscle. To induce spawning, 0.4 mℓ of the 2-mM serotonin solution was hypodermically injected into the anterior adductor muscle.

Both individual and mass spawning techniques as described by Castagna and Kraeuter (1981) were utilized without any thermal shock or other stimulation to spawn ocean quahogs. All spawning experiments were conducted at a salinity of 32 ppt and at a controlled temperature of 15–16°C. Ocean quahogs were spawned by placing single specimens in glass dishes containing 1ℓ of 1-μm-filtered seawater. Mass spawning was achieved by placing the quahogs in troughs containing 140 ℓ of static, 1-μm-filtered seawater. Equal numbers of quahogs in the control groups were treated in the same manner as the test groups except they were injected with 0.4 mℓ of 1-μm-filtered seawater instead of the serotonin solution. The control animals from trial 1 of the mass spawning were the test group for trial 2. The G-test of independence and Williams' correction for a 2 × 2 contingency table were used to statistically determine

whether spawning was independent of injection with the serotonin solution (Sokal and Rohlf 1981).

Eggs obtained from the serotonin-induced spawnings were fertilized using standard techniques developed for other bivalves (Loosanoff and Davis 1963, Castagna and Kraeuter 1981). Eggs were not pretreated with ammonium hydroxide or other chemicals prior to fertilization. The larvae were reared through settlement and metamorphosis to early post-set at 13.5°C.

RESULTS AND DISCUSSION

Injection of the serotonin solution induced gamete release in both the individual and mass spawning trials, although greater percentages (35.5% and 37.1%) of ocean quahogs spawned using the mass spawning technique than for the individual method (17.1% and 22.5%) (Table 1). In each case larger numbers of quahog males spawned than females. This, however, may be a dose response. Ocean quahogs injected with serotonin extended their siphons, probed with their feet, and began spawning within 15 minutes. The control groups injected with filtered seawater did not exhibit any of these behavioral patterns and did not spawn.

The egg capsules of the ocean quahog are unlike any structures described for bivalves (Castagna et al. 1982). The encapsulated eggs were slightly ovoid and ranged from 75.0 to 85.0 μm in diameter ($\bar{X}$ = 79.9 μm; S.D. = 1.3 μm). Fertilization occurred in mass spawnings and similarly upon addition of sperm in individual spawnings without chemical pretreatment of the freshly spawned eggs. The egg capsules have been suggested as being responsible for the difficulty in spawning ripe ocean quahogs or in fertilizing stripped eggs (Lutz et al. 1982), but no difficulty was observed with this technique. Exposure of stripped eggs to ammonium

hydroxide may result in a lower percentage of normally developing larvae compared to naturally spawned eggs (Loosanoff and Davis 1963). Serotonin-induced spawning appears to be a more effective means of obtaining gametes from ripe ocean quahogs than stripping gametes from mature individuals.

The development of larvae from the trochophore stage through metamorphosis was similar to that described for larvae of this species obtained from fertilization of stripped eggs (Landers 1976; Lutz et al. 1981, 1982). Developing eggs were encapsulated up to the gastrula stage, at which time the egg capsules were lost. Metamorphosis occurred at shell lengths of 170.6 to 266.7 μm ($\bar{X}$ = 220.5 μm; S.D. = 19.8 μm) between 37 and 62 days after natural fertilization, which was similar to results obtained by others for fertilized stripped eggs (Landers 1976, Lutz et al. 1982).

To date, serotonin has been effectively utilized to induce spawning in several species of bivalves (Matsutani and Nomura 1982, Gibbons and Castagna [in press]). It is a neurotransmitter that occurs naturally in the cerebropleural, pedal, and visceral ganglia of *Arctica islandica* at concentrations of 20 μg · g fresh tissue^{-1} (Welsh and Moorhead 1960). In laboratory studies, serotonin has been found to excite excised hearts of ocean quahogs by stimulating the cardioregulatory nerves (Gaddum and Paasonen 1955, Leake and Walker 1980). The physiological role of serotonin as an inducer of spawning in bivalves is unknown.

The use of serotonin has induced spawning in the ocean quahog, a bivalve that historically has been difficult to spawn in the laboratory. Serotonin has potential value to induce spawning in other bivalves which are resistant to conventional spawning stimuli. The advantages of this technique include ease of use and rapid and synchronous spawning of ripe individuals.

TABLE 1.

Numbers of ocean quahogs induced to spawn by injection of serotonin.

Spawning Technique	Treatment	Number Tested	Number Spawned	Percentage Spawned	Number Males	Number Females
Individual – trial 1	Serotonin	35	6*	17.1	5	1
	Control	35	0	0	0	0
Individual – trial 2	Serotonin	40	9*	22.5	7	2
	Control	40	0	0	0	0
Mass – trial 1	Serotonin	35	13*	37.1	10	3
	Control	35	0	0	0	0
Mass – trial 2	Serotonin	31	11	35.5	10	1

*significant at P <0.005.

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COVER PHOTOGRAPH (1.5 ×):   Florida rock-shell *Thais haemastoma floridana* (Conrad), also known as the "southern oyster drill," on shell of the eastern oyster *Crassostrea virginica* (Gmelin). Note the drill hole on the small attached oyster. Specimens were collected from Biloxi Bay, Mississippi. [Photograph taken by Dr. Robin Overstreet and printed by Joan Durfee, Gulf Coast Research Laboratory, Ocean Springs, MS.]